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IMPACTS OF CHANGING INSHORE WATER TEMPERATURES ON PHENOLOGY AND THERMAL PREFERENCES OF FISH SPECIES

BY

M. ELISABETH HENDERSON

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE

REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

IN

BIOLOGICAL OCEANOGRAPHY

UNIVERSITY OF RHODE ISLAND

2013

MASTER OF SCIENCE THESIS

OF

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UNIVERSITY OF RHODE ISLAND
2013

ABSTRACT

The University of Rhode Island Graduate School of Oceanography Fish trawl survey of Narragansett Bay, Rhode Island, USA, provides a unique weekly time series of fish and invertebrate abundances over the last five decades (1959-present). Conditions in the bay changed in numerous ways since 1959 including increasing sea surface temperature and declining chlorophyll concentrations. With rising ocean temperatures, fish species may change phenology, abundance, or physiologically adapt to differing temperature regimes.

A comparison of species distributions according to water temperature and week of year is made with single-parameter quotient analyses to assess the magnitude and patterns of temporal changes. Species that usually inhabit the bay during the winter, spring, and early summer shifted towards later seasonal distributions in recent years; fall species shifted towards earlier seasonal distribution. In general, pelagic-feeding species' abundances increased while demersal-feeders declined. Results suggest species alter phenology and thermal preferences to follow changing seasonal distribution of chlorophyll, used as a proxy for bay production. The small spatial scale of this study allows for better examination of local variability in fish species' responses to ocean warming relative to similar regional studies.

ACKNOWLEDGMENTS

First, my thanks go to my major advisor, Jeremy Collie, whose patience and subtle guidance brought me to this point. My other committee members, Candace Oviatt and Jon Hare, also offered invaluable advice and support throughout this project.

My thanks also to the URI Graduate School of Oceanography (GSO) for funding the GSO Fish trawl. The Fish trawl would also not be possible without the support of over five decades of graduate assistants working in the bay. Their dedication and consistency contributes to the longest running trawl survey in the United States. Special thanks to Anna Malek and Rich Bell for their time and advice on numerous occasions. And to Tom Puckett, captain of the R/V Cap'n Bert, who has been my Monday morning companion for the past two-and-a-half years. I am grateful for his patient deckhand mentoring, insightful conversation, and insider seafood tips.

Finally, thanks to my family for nurturing my passion for the ocean. Your honest enthusiasm for my endeavors and patient, often confused, head nods lent much needed encouragement along the way. And to Chris Chambers, who continues to support me wholeheartedly in my pursuits.

PREFACE

This thesis is compiled in manuscript format, in accordance with the URI Graduate School guidelines for thesis preparation. This text will be formatted for submission to a journal with co-authors Jeremy Collie, Jon Hare and Candace Oviatt. There is one appendix of supplemental methods.

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CHAPTER 1

INTRODUCTION

Several impacts of climate change are predictable including rising global temperature, one of the most influential to marine ecosystems (Portner and Farrell 2008; Rozenzwieg et al. 2008). Historical evidence shows that global temperature rise in the last 50 years is nearly twice that of the last 100 years (IPCC 2007). Models predict that the rate of temperature rise will continue to increase in the future. Even modest rate assumptions for future greenhouse gas emissions predict global temperatures to rise at 0.1-0.2°C per decade (Trenberth et al. 2007).

Global mean sea surface temperature increased by 0.67°C over the last century (IPCC 2007). At the regional level, sea surface temperature in the Northeast US Continental Shelf Large Marine Ecosystem (NES LME) increased by 0.23°C from 1982-2006, a 14-year period (Belkin 2009). A compiled temperature record from Woods Hole, Massachusetts, shows no trends in water temperature from 1886-1946 followed by a significant warming period from 1970-2002 at a rate of 0.04°C yr^{-1} (Nixon et al. 2004). Changing water temperatures can affect local fisheries depending on a combination of factors including species-specific traits (Friedland and Hare 2007). Species-specific traits determine, in part, the changes that manifest including geographic distribution shifts and physiological adaption.

Numerous studies of terrestrial and some marine systems, indicate that populations follow thermal habitats as they move towards the poles. As a result of this process coined ‘tropicalisation’ by Cheung et al. (2012), warmer-water species will

become increasingly dominant in marine communities. Tropicalisation has been observed within the NES LME (Lucey and Nye 2010) and at the local level in the Long Island and Rhode Island Sounds (Howell and Auster 2012; McLean 2006).

Species might also adapt to a changing thermal environment to remain within the same geographical range. Studies of temperature preference indicate that species' temperature of occurrence warm as their habitats warm (Collie et al. 2008; Cheung et al. 2010; Pinsky and Fogarty 2012). Climate change also influences phenology (Edwards and Richardson 2004). Species could alter seasonal migration patterns to accommodate strict temperature preferences while maintaining the same range. Given either of these adaptive strategies for increasing temperatures, similar species assemblages would occur but the thermal and seasonal preferences may change.

The University of Rhode Island Graduate School of Oceanography (GSO; Narragansett, Rhode Island, USA) fish trawl survey provides a set of weekly bottom trawls and sea surface temperatures since 1959. Since 1959, warming temperatures have correlated with changing species assemblages in the bay (Collie et al. 2008). Collie et al. (2008) used weighted mean temperatures as a metric to assess species in the trawl data. Although useful, this method is imperfect because it is based on literature values for optimal species preferred temperatures; it does not account for the temperatures available in the sampled area. Many species exist at temperatures other than that optimal for their physiology.

This study uses a metric of preference based on the ambient temperatures at which species were observed weighted by species abundance, and compared to the temperature sampling distribution, similar to Rockmann et al. (2011) and Twatwa et

al. (2005). The same principle was applied to species' phenologies, or seasonal preference, by week of year. As temperatures in the bay increase, species were expected to follow preferred temperatures either by changing phenology or altering geographical distributions. A change in geographical distribution would be evident in changing species abundances. As population centroids move to higher latitudes, catch per tow abundances in Narragansett Bay should decline. Conversely, species with warmer preferences might move into the bay, thereby becoming more plentiful.

CHAPTER 2

METHODS

Data

The GSO trawl began conducting weekly bottom trawls of two stations in Narragansett Bay, Rhode Island in 1959. One station is located in the mid-bay, east of Fox Island, at an average depth of 7 meters; the other station is located in the lower bay, near Whale Rock, at an average depth of 23 meters (Fig. 1, Collie et al. 2008). Since the trawl began, several vessels have been used: *F/V Billie II* (13 January 1959 – 28 June 1977), *F/V Dulcinea* (28 June 1977 – 16 July 1982), *F/V Gail Ann* (16 July 1982 – 8 September 1987), and *R/V Cap'n Bert* (8 September 1987 – present). Surface and bottom water temperatures are also recorded at each station. A Niskin bottle and bucket thermometer was used until 2006; since then a conductivity, temperature and depth (CTD) probe (YSI 6920 V2 - 2) has been used. Surface temperature records are used in this study because the bottom temperature time series is incomplete.

Otter trawl nets and towing procedures remained consistent throughout the time series. The trawl net has a bottom sweep of 15.2 m and cod-end mesh size of 5.1 cm (Collie et al. 2008; Tom Puckett, University of Rhode Island, Kingston, RI 02882, USA, personal communication). The trawl doors are 1.52 x 0.76 m and attached 18.2 m from the net mouth. Winches let out 36.5 m of cable at Fox Island and 82 m at Whale Rock. For each station, the net is towed north to south at a speed of 2 knots for 30 minutes, spanning about 1 nautical mile (1.8 km).

Chlorophyll data and analyses

Temporal trends in chlorophyll-a seasonality were assessed using data from two stations. One station corresponds to the same mid-bay station, Fox Island, used for the GSO trawl. Complete years of data were available 1973-1996 (Li and Smayda 1998; *http://www.narrbay.org/d_projects/plankton-tsv/plankton-tsv.htm*) and 1999-2011 (*http://www.gso.uri.edu/phytoplankton/*). The other is a lower bay station located at the URI GSO pier; complete years of data were available 1977-2011 (*http://www.gso.uri.edu/merl/data.htm/*).

Earlier data from Fox Island required some conversions to compare with more recent methods. Data from Li and Smayda (1998) were standing stock measurements (mg/m^2). These measurements were integrated over the 8m mean depth of the well-mixed water column to approximate concentrations (µg/L) (Li and Smayda 1998; Borkman and Smayda 1998). Additionally, chlorophyll samples collected prior to 2008 at the Fox Island site were frozen. A correction for sample degradation was applied (Graff and Rynearson 2011; Fields 2013).

A number of tests were performed to compare the seasonal and thermal distribution of chlorophyll temporally and spatially in the bay (Appendix A-1). A modified Kolmogorov-Smirnov test using randomly generated maximum distances was used to compare the first and second halves of each station's time series (see pages 16-17). For each station, the observed d_{max} between cumulative distributions of chlorophyll concentration by weeks and temperature was compared to a distribution of randomly generated d_{max}. Temporal trends in annual and seasonal mean chlorophyll

were assessed using log-transformed regressions of annual mean chlorophyll concentration at each station.

Analyses

The GSO trawl-survey database contains records of 139 species; the twenty-five most abundant and frequently observed species from the years 1961 – 2012 were used in this study. The years 1959 and 1960 were excluded in order to assess the time series in 4 segments of equal length (13-years). Each of the 25 species chosen were present in at least 49 years. Though species abundances varied over the time series, this subset represents 94% of over 2.1 million animals recorded.

Weekly sampling was missed occasionally for poor weather conditions and boat repair. Additionally, some tows do not have corresponding surface temperatures. Because temperature preference is a focus of this study, only tows paired with surface temperature records were used. Despite these constraints, there were few large gaps in sampling such that nearly every month of every year was sampled. Of 624 months, 9 months at Fox Island and 28 at Whale Rock contained no tows paired with temperature. All other months contained one or more tows with temperature at each station; 96% of months at Fox Island and 94% of months at Whale Rock contained two or more tows with temperature.

We used single parameter quotient (SPQ) analysis to describe the distribution of a given species with respect to an environmental parameter – in this case, surface temperature or week of year. Surface temperature was binned by degree Celsius and day of year was binned by week of year. Week of year sampling was very consistent

(Fig. 1); nearly all years contained once weekly sampling. Temperature sampling was more variable. Single parameter quotient analyses control for sampling variation by dividing the proportion of the population, *a*, in each parameter bin, *b*, over the proportion of samples, *s*, taken in that bin (Payne 2008).

$$Q_b = \frac{\frac{a_b}{\sum_p a_p}}{\frac{s_b}{\sum_p s_p}}$$

The quotient, Q_b, is a relative term, unique to each species and parameter. Quotients are standardized by dividing the quotient by the sum of quotients in all bins for that parameter, sQ_b. Standardized quotients are then used to compare species preferences for temperature and week of year.

$$sQ_b = \frac{Q_b}{\sum_p Q_p}$$

Cumulative distributions of each standard quotient describe the weeks and surface temperatures corresponding to the 25th, 50th and 75th percentiles of each species' parameter preference. The 50th percentile describes the parameter value at which point the median abundance of a species is observed, also called the median preference. The difference between the 25th and 75th percentiles describes a species' parameter specificity for a particular range of temperature or seasonal timing at either station in Narragansett Bay. Species that are more selective have narrower parameter specificity ranges. It is important to note that quotient analyses are based on relative abundances. Therefore, quotients generated from particularly low total abundances might not accurately reflect true preferences.

General preferences

Each species' general parameter preferences from 1961-2012 were calculated. Median preferences (50^{th} percentile) and preference selectivity ranges (25^{th}-75^{th} percentiles) were calculated from temperature and week SPQs. General preferences for temperature are particularly useful for thinking about the species that might be most immediately affected by changing temperatures in the bay. Species with colder preferences are more likely to spend less time in Narragansett Bay when the temperatures exceed their physiological limits. Likewise, warm-water species could become more abundant as the bay's thermal environment becomes more favorable.

Two-sample Kolmogorov-Smirnov tests

To evaluate the potential significance of the SPQ analyses, modified standard two-sample Kolmogorov-Smirnov tests were used. The cumulative distributions of abundances from the two halves of the time series used for SPQ analyses (1961-1986 and 1987-2012) - binned by degree Celsius or week of year- were calculated for each species. The absolute value of the maximum distance between the two distributions is known as the Kolmogorov-Smirnov test statistic or d_{max}. A critical distance value, d_{crit}, is then subtracted from the maximum distance to produce an F statistic.

In a typical Kolmogorov-Smirnov test, the critical distance value is calculated from the sampling abundance of the two distributions, n_1 and n_2 (1961-1986 and 1987-2012 respectively), and using a 95% confidence interval that corresponds to a table value. In this case, the number of tows taken in a given parameter bin is the sampling

abundance, n, for each half of the time series. Distributions with d_{max} greater than d_{crit} are deemed significantly different.

This study used a modified Kolmogorov-Smirnov test based on different critical distance values. For a given species, station and parameter combination, the time series was divided in half by years randomly and a d_{max} was generated. This process was repeated one thousand times and the series of d_{max} were stored in a vector. This vector yielded a one-sided probability distribution of randomly generated d_{max}. The 95% interval of this distribution is calculated and used as the new critical value for maximum distance (see Appendix A-2). The new d_{crit} provided a more strict assessment of species distributions according to temperature and weeks.

This test was considered more applicable to the distributions in question because a typical Kolmogorov-Smirnov d_{crit} is based on just one sampling event for each cumulative distribution. Each of the cumulative distributions used here comprised 26 years of weekly sampling. The modified test was a more realistic comparison for the observed maximum distances between chronologically divided years.

Median preference shifts

To assess changes in preference over time, the time series was divided into two halves, 1961-1986 and 1987-2012. The time series was further divided into 4 segments of equal length; 13 years was determined appropriate to capture variability on a shorter interval while maintaining sufficient sampling within each temperature degree bin in a given segment of years. Standard quotients for surface temperature

and week of year preference were calculated for each half of the time series and each of the 4 segments.

Fixed Preferences

Five hypothetical species were created for the purpose of null parameter preference calculations. Five of the dominant species median preferences and preference ranges across the whole time series (1961-2012) were chosen to represent the mean seasonal temperature distribution. These five null species were intended to illustrate the anticipated changes in parameter preferences for species occurring during certain seasons given the changes in weekly temperature distributions between the first and second halves of the time series.

Quotient parameter preferences were generated for model null species to indicate the expected shifts in parameter preferences over the time series assuming that a species either: 1) changed seasonal preference to follow the same temperature preferences or 2) changed temperature preference to follow the same seasonal preference.

Quotients for model species with unchanged week preference were calculated by generating the quotients for temperature and week of year preference from the first half of the time series. The week preference would remain constant for the second half of the time series.

Temperature quotients for species with unchanged week preference were calculated by aggregating the weekly abundance for each time segment into the corresponding temperature bins, j, for that segment to derive the abundance by

temperature degree bin distribution, a_j. The sampling distribution for temperature degree bins is more concentrated in the colder and warmer temperatures and also changed across the time series (Fig. 1) therefore the sampling distribution used in the quotient numerator is unique to each half of the time series. The temperate quotient is then calculated in the normal way according to equation 1.

Quotients for model species with unchanged temperature preference were calculated by generating the quotients for temperature and week of year preference from the first half of the time series. The thermal preference would remain constant for the second half of the time series.

Week quotients for species with unchanged temperature preference required a more creative approach. First, the species abundance by temperature distribution was derived by multiplying the thermal preference quotient by the temperature sampling distribution (Fig. 1).

$$Q_j^t \times \frac{s_j}{\sum s_j} = \frac{a_j}{\sum a_j}$$

Because temperature bins can occur during more than one week of the year, a probability matrix of temperature degree bins versus week bins, $P_{i,j}$, was generated using the distributions of temperature and week sampling for each half of the time series. The weekly abundance was calculated by multiplying $P_{i,j}$ by the abundance by temperature distribution. This abundance by week is then equivalent to the week of year quotient for species with fixed thermal preferences.

$$\frac{a_i}{\sum a_i} = P_{i,j} \times \frac{a_j}{\sum a_j}$$

Parameter selectivity metric

The parameter selectivity metric captures changing parameter selectivity between the first and second halves of the time series by dividing the parameter selectivity of the later half by the parameter selectivity of the first half. If the quotient is greater than 1, the parameter selectivity increased; a quotient less than 1 indicates a decreasing range of parameter selectivity.

Interdecadal variation metric

A segment metric was generated using the median preferences for the four 13-year time segments (1961-1973, 1974-1986, 1987-1999, 2000-2012) to assess the linearity of species' changing median preferences over the time series. The sum of the magnitude of change between each of the four median preference values, q_{50}, for temperature or week is divided by the sum of the magnitude of change between the first and last or the net change across all four segments, q_{50}*.

$$M = \frac{\sum_{1,2,3} q_{50}}{q_{50}*}$$

For median preferences with the same direction of change between all four segments, the metric will equal one. If the metric value is greater than one, the direction of preference change is not linear between the first and fourth time segments. If the metric value is close or equal to one, the direction of preference change is assumed to be nearly the same throughout the time series.

Mantel tests

To compare the distribution of species abundance and chlorophyll concentration, a series of Mantel tests were performed. The tests used tables of weekly species abundances and chlorophyll concentrations by years to calculate Euclidean distance matrices. Distance matrices of chlorophyll and species abundances were then compared for similarity.

2012: The hottest year

The warmest year, 2012 provides a potential platform to examine effects of climate change and warming, similar to preexisting models of long-term scenarios. In 2012, the Northwest Atlantic Ocean warmed more than it has in the last 30 years (see Figure 1a, Mills et al. 2013). Narragansett Bay water temperatures also warmed considerably (Fig. 17; Fig. 18). Catch abundance of the top 25 species in 2012 was compared to the five preceding years (2007 - 2011). A similar comparison was made using warm water species to look for increased warm water species presence in the bay during extreme warming.

CHAPTER 3

RESULTS

First, an initial assessment of sea surface temperature and chlorophyll is presented to establish a basic understanding of Narragansett Bay over the past five decades. Next, single parameter quotient analyses and species abundances provide a platform to assess temporal changes in phenology, thermal preferences, and geographic distribution of fish and invertebrate species since 1961. The hottest and most recent year, 2012, is used as a basis for predicting the future of Narragansett Bay under present climate warming conditions. These analyses are finally interpreted in the context of recent literature.

Sea surface temperature trends

Seasonal sea surface temperature at both stations increased by about 2°C since 1961 (Fig. 2). All mean seasonal temperatures were lower during the 1960s; this cooler decade was not as apparent in the spring mean temperatures. The shallower, upper bay station, Fox Island, is typically warmer than the sound station during the spring and summer months (Fig. 2c, Fig. 2d). Whale Rock is warmer in the winter months (Fig. 2b). The more shallow water column in the mid-bay has a lower heat capacity and therefore warms and cools more quickly than the sound station. Mean fall sea surface temperatures are similar at both stations (Fig. 2a).

Mean weekly sea surface temperatures for each of the four time segments were subtracted from the time series mean weekly temperatures at each station (Fig. 3a; Fig. 3c) and for each half of the time series (Fig. 3d; Fig. 3d). The temperature anomaly for each segment indicates the extent to which the weekly mean temperature deviates from the time series mean. The first and last 13-year segments (Fig. 3a; Fig. 3c) represent the most extreme anomalies while the middle two segments represent a range of weekly temperatures much closer to the time series means. The most recent years (2000-2012) indicate warmer temperatures by over 0.5°C above the time series mean for most of the year; however late spring and early summer months (March-July) have a much lower magnitude anomaly, containing values closer to, but still above, the time series mean. The middle time segments (1974-1986 and 1987-1999) do not deviate more than 0.5°C from the time series mean during any week of the year. The earliest time segment (1961-1973) was a much cooler period than the rest of the time series, deviating by about 1°C below the time series mean in late winter and early spring (March-May).

The middle time segments moderated the mean weekly sea surface temperature anomalies for each half of the time series (Fig. 3b; Fig. 3d). Anomalies at either station hardly exceeded 0.5°C. At Fox Island, the mean temperatures in summer and fall were the most similar between the two 26 year periods while the winter and early spring were the most different. Mean winter and early spring temperatures before 1987 were on average nearly 1°C cooler than after; at Whale Rock, the difference was slightly greater. Late fall temperatures at Whale Rock were the most similar between the two 26-year periods with a difference less than 0.5°C.

Chlorophyll analyses

Mean chlorophyll concentrations near Fox Island (mid bay) and the GSO dock (lower bay) indicate that temporal trends varied spatially (Fig. 4a). Fox Island decreased from the 1970s through the early 1990s. When the time series picked up again in 1999, annual mean concentration dropped by over half; mid-bay chlorophyll continues to decline through the present (Fig. 4). Concentrations in the lower bay were consistently lower and less variable relative to the mid-bay over the past five decades.

Weekly chlorophyll distributions at Fox Island and the GSO dock station differed significantly ($p=0.048$, $K=0.096$; Fig. A-1). The Fox Island station generally decreased whereas the lower bay station remained relatively constant. Seasonal variation in the upper bay also diminished in recent years. The winter-spring bloom declined and the summer-fall bloom shifted to slightly later time of year (Fig. 4b). However, the modified Kolmogorov-Smirnov tests (Appendix A-1) indicate neither station's weekly distribution of chlorophyll changed.

Regression analyses indicate greater variability in annual and seasonal mean chlorophyll concentration in the mid-bay than the lower bay (Fig. 5; Fig. 6). Despite large scatter, annual ($p=0$, $R^2=0.289$), fall ($p=0.031$, $R^2=0.104$), and winter ($p=0.015$, $R^2=0.133$) mean chlorophyll concentrations had decreasing trends at Fox Island. No significant annual or seasonal trends were detected at the GSO dock station (Fig. 6).

Cumulative chlorophyll distributions by temperature degree compared using standard Kolmogorov-Smirnov tests revealed significant differences between the mid

and lower-bay stations (Fig. A-1). In the randomly generated maximum distance test, neither station's distribution according to temperature changed significantly over time, although Fox Island was close to significant ($p=0.056$, $K=0.097$; Fig. A-3; Fig. A-4).

Catch abundance trends

Abundance of the top 25 species increased in the latter half of the time series at both stations (Fig. 7). At Fox Island, increased abundance occured more in the early summer (May-June) and late summer (August-September). As a result, the 25th and 50th percentiles shifted by approximately three and four weeks respectively (Fig. 7c). The 75th percentile changed little over time. In general, Fox Island abundances shifted later in the year, with a higher proportion of the catches occurring in summer months. At Whale Rock, the seasonal proportion of abundance did not change much before the 50th percentile in August (Fig. 7d). The 1987-2012 cumulative proportion reached the 75th percentile about four weeks earlier than the 1961-1986 segment; the catch abundance increased in the late summer during the second half of the time series.

Two-sample Kolmogorov-Smirnov tests

The modified two-sample Kolmogorov-Smirnov test, using randomized time series divisions to determine a critical distance value, indicated few species with significant changes in distribution according to degree Celsius or week of year over the time series (Table 1). In general, distributions at Fox Island were more likely to be significantly different than distributions at Whale Rock. Observed species distributions at Whale Rock were more closely related to the randomized distributions.

General preferences

General preferences for week of year (Fig. 8) indicate that most species preferred to inhabit the bay during the early spring through early fall. Few species at either station had median preferences in the late fall and winter (e.g., Atlantic herring, longhorn sculpin). Species' general seasonal preferences at Whale Rock indicate similar preferences but often offset from those at Fox Island by a few weeks in either direction (Fig. 8; Fig. 9a).

Species with wide seasonal ranges include cancer crabs, windowpane flounder, little skate, fourspot flounder, winter flounder, spider crab, red hake, silver hake, and blueback herring. Species with narrow ranges, from about 8 to 12 weeks include tautog, northern searobin, summer flounder, conch, longfin squid, smooth dogfish, butterfish, horseshoe crab, and weakfish. Atlantic herring, northern kingfish, alewife, and longhorn sculpin have the narrowest ranges, less than 8 weeks.

General preferences by temperature indicate thermal preference ranges corresponding to the mean weekly temperatures during the preferred week ranges (Fig. 10). This information delineates species that prefer the extreme cold and warm temperatures in Narragansett Bay. Species' thermal preferences were similar but slightly warmer at the shallower, mid-bay station (Fig. 9a). Species that preferred warmer temperatures at either station were squid, summer flounder, butterfish and conch while the species with colder temperature preferences include Atlantic herring and both sculpin species.

Hypothetical preference shifts

The hypothetical species with fixed preferences exhibited a variety of responses (Fig. 11). For the species with fixed week of year preferences, the shifts in thermal preference in the second half of the time series were modest, similar to the modest shifts in mean weekly sea surface temperature. The species with fixed thermal preferences exhibited larger shifts in week preference, up to nearly 7 months for the mid-bay station.

Median preference shifts

Single parameter quotient (SPQ) analyses used in this study indicate preferences for temperature and weeks based on abundance corrected by the parameter sampling distribution. Single parameter quotients were assessed for the first and second halves of the time series to compare general changes in temperature and seasonal preference in the last 5 decades (Fig. 12). Several vectors represent counterintuitive preference shifts. For example, the magnitude and direction of change of some vectors did not relate to the change in weekly temperature between the first and second halves of the time series. These vectors also corresponded to species whose distributions according to temperature and weeks did not shift significantly according to the Kolmogorov-Smirnov tests (Table 1; Appendix A-3).

Vector changes in temperature and week of year median preference between the first and second halves of the time series indicate several varieties of preference shifts. Vectors with little vertical change indicate little change in median temperature

preference. Likewise, vectors with little horizontal change indicate less change in median week preference.

Most species at the Fox Island station shifted temperatures and week of year preferences relatively close to the mean surface temperature by week for each half of the time series. Median preference shifts at the Whale Rock station were not synchronous with those indicated at Fox Island. Although colored vectors indicate species whose distributions were significantly different (Table 1), they do not follow the mean weekly temperature curve. Additionally, the direction and magnitude of changes do not relate to those indicated by species at Fox Island. A comparison of the preference shifts between the two stations indicated no spatial correlation (Fig. 13). Species at Whale Rock had greater changes in thermal preference whereas Fox Island tended towards larger week of year preference changes. Lack of correlation in preference change between the two stations is a contrast to species' general preferences, which were spatially auto-correlated (Fig. 9).

Species' rates of abundance change and general median thermal preference were not significantly related at either station (Fig. 14). There was no apparent relationship between the change in abundance and the change in preference for temperature or week of year at either station.

Parameter selectivity

Species' ranges of preferred temperatures and weeks changed since 1961 as well. The parameter selectivity metrics (Table 3) indicate whether the range of selectivity increased (greater than 1), decreased (less than 1) or remained constant

(equal to 1) over the time series. Some species appear to sacrifice, or decrease, selectivity in one parameter, either temperature (D_t) or week of year (D_w), to increase selectivity in the other parameter. A number of species at Fox Island (Atlantic herring, horseshoe crab, little skate, lobster, longfin squid, and smooth dogfish) decreased temperature preference range while increasing week of year range. Conversely, other species (blueback herring, butterfish, red hake, tautog, and weakfish) decreased temperature selectivity in favor of a narrower range for week of year.

Interdecadal variation metrics

The median preference vectors (Fig. 12) summarize changes in temperature and week preferences between the first and second halves of the time series. However, mean weekly temperatures for the time series split in half (Fig. 3b) hide much of the variation that is shown by the time series in smaller segments (Fig. 3a).

A metric value equal to 1 (e.g., Winter flounder) indicates that the direction of shift has not changed during the four 13-year time segments (Table 4). Metric values greater than 1 indicate that the direction of shift changed. Metrics much greater than 1 typically correspond with species, station and parameter combinations for which the Kolmogorov-Smirnov tests (Table 1) indicated no significant change in distribution over the two halves of the time series.

Mantel test

Mantel tests of similarities between species and chlorophyll in the bay revealed few significant relationships (Table 5). The only species with significant relationships were demersal and invertebrate species except for blueback herring at Whale Rock. All significant relationships were also positive meaning that species abundances and chlorophyll concentrations were positively related.

2012: The hottest year

Narragansett Bay water temperatures during the winter, spring, and summer of 2012 were almost consistently 2 to 3°C warmer than the rest of the time series or the five preceding years (Fig. 16; Fig. 17). The comparison of catch distributions between 2012 and the five preceding years indicated an earlier distribution in 2012 at both stations (Fig. 18); at Whale Rock, catch distribution shifted nearly 4 weeks earlier (Fig. 18d). In general, seasonal distribution at Fox Island is more variable.

A similar comparison of the warm-water species (Table 6) did not indicate particularly unique differences, as warm water species abundances are typically much lower than for dominant species (Fig. 19). Warm-water species seasonal distribution at Whale Rock shifted earlier in the year. Fox Island changed little; differences are hard to decipher due to the low sample sizes.

CHAPTER 4

DISCUSSION

This study attempted to find evidence for fish and invertebrate species' responses to warming water temperatures since 1961 through adaptation, altered phenologies, and changing abundances. Results suggest that species' responses to warming water temperatures in Narragansett Bay are more complicated than the hypotheses presented in this study (Table 7).

Chlorophyll

Chlorophyll temporal trends varied spatially in the bay with greater annual and inter-annual variation near Fox Island than Whale Rock. Concentrations near Fox Island, in the mid-bay, declined annually whereas concentrations near Whale Rock, in the lower bay, remained relatively consistent. Chlorophyll seasonality changed at Fox Island whereas at Whale Rock, there was no significant change.

Evidence suggests that chlorophyll at Fox Island is limited by zooplankton grazing while the lower bay, near Whale Rock, is nutrient limited (Oviatt et al. 2002; Li and Smayda 1998). Furthermore, the level of grazing is probably associated with water temperature (Li and Smayda 1998). With warming water temperatures, metabolic requirements increase causing zooplankton to take advantage of the abundant phytoplankton in the mid-bay, particularly in the winter during the period of the winter-spring diatom bloom. When zooplankton grazing limits phytoplankton,

most primary production remains in the water column, rather than sinking to the bottom as detritus. Therefore, less food is available to benthic infauna that is also prey for many benthic species.

Warming water temperatures are also associated with earlier and increased seasonal abundances of comb-jellies (*Mnemiopsis leidyi*) in the bay (Sullivan et al. 2001). The summer-fall diatom bloom may persist in recent years because comb-jellies consume vast quantities of zooplankton, allowing phytoplankton to bloom in late summer. However, as temperatures cool again in the fall, comb-jellies leave the bay, allowing zooplankton to graze on the diatom bloom.

Given the above hypotheses, years with increased grazing and lower chlorophyll would have fewer demersal and invertebrate species that depend on organic matter reaching the benthos. Indeed, as Collie et al. (2008) indicated, the pelagic-demersal ratio of fish increased over the last five decades. Furthermore, fish abundances in the bay also increased. Pelagic species, including butterfish, that consume comb-jellies and other zooplankton, may be taking advantage of more abundant food in the water column. Conversely, demersal-feeders suffer diminished food availability as less primary production sinks to the benthos.

The zooplankton-grazing hypothesis also explains why, in the latter, warmer half of the Fox Island time series, fall seasonal chlorophyll decline was more rapid (Fig. 4b). Increased zooplankton metabolic needs could cause the phytoplankton to be grazed down much faster than in earlier years.

Phenology and thermal preferences

General phenology and thermal preferences were spatially correlated between the two stations. Thermal preferences at Fox Island tended to be a little warmer than Whale Rock. The shallower water column at the mid-bay station reaches warmer temperatures that are favored by warm-water species.

Overall, observed preferences for temperature and week suggest that species do not respond directly to warming. Mean weekly temperatures in the bay changed marginally between the two 26-year segments; this suggests that species preference for temperature and week would also change little. Indeed, the model species with fixed week of year preferences exhibit marginal median preference changes, similar to the mean weekly temperature (Fig. 11). However, the model species with fixed thermal preferences exhibited a very different response. Certain temperatures occur at more than one time of year. The P_{ij} matrix calculates probabilities for given temperature degree bins occurring in each week of the year. If the probability of a temperature degree bin is greater in the spring than in the fall, the quotient for thermal preference will shift towards the spring; this was exhibited for one fall species in particular (Fig. 11). Species occurring closer to the peak of the mean weekly sea surface temperature curve experience a similar confounding effect.

The observed species exhibited very different responses to warming water temperatures in the latter half of the time series (Fig. 12). Alewife, Atlantic herring and blueback herring changed phenology towards much later in the year. This shift was nearly exactly opposite of the predicted direction of shift for species with fixed thermal preferences in the same temperature ranges. In other words, species did not select preferences based exclusively on temperature. If they had, phenologies would

shift towards the week of year that has the highest probability of a preferred temperature occurring. In general, seasonal preferences shifted towards the early fall and warmer temperatures. These preferences also align with the mean summer-fall chlorophyll bloom (Fig. 4).

This study also hypothesized that abundances would change as populations move northward to track preferred temperatures. Species with colder preferences would decline while species with warmer preferences became more plentiful in the bay. The relationship between species' general thermal preferences and the annual rate of species abundance change was not significant at either station (Fig. 14). However, the regression at Whale Rock ($p=0.078$) suggests that there may be a slightly positive, albeit insignificant, relationship.

If species were shifting distributions into or out of the bay, we would expect to see larger rates of change in species abundances correspond to smaller changes in single parameter quotients. Alternatively, if species were adapting to temperatures in the bay, we would expect smaller species rates of change correspond to larger changes in preference. There was no strong evidence of these processes occurring (Fig. 15). Most species had modest rates of change in abundance associated with modest changes in median preferences. However, some species at Fox Island with large rates of abundance change also had small to no change in week of year preference (Fig. 15b). Additionally, some of the species with little change in abundance had relatively larger jumps in week of year preference. This corroborates Figure 12a that indicates species at Fox Island tended to shift phenology. Thermal preferences at Whale Rock

suggest a similar trend (Fig. 15c); this also supports Figure 12b wherein species at Whale Rock tended to have greater shifts in thermal preference than phenology.

A comparison of the magnitude and direction of shifts in median preference between the two stations suggests that the changes in species preferences observed in the mid and lower bay are not related (Fig. 13). Species tended to shift thermal preferences more at Whale Rock than at Fox Island. Conversely, species at Fox Island shifted week preference more than species at Whale Rock.

Overall, species' phenologies and thermal preferences did not shift as anticipated in this study. Several other factors may have contributed to these results. Primary production, general thermal and seasonal preferences, and trophic levels may work together to produce observed species distributions in Narragansett Bay.

Differences between the mid and lower bay

Differences at Whale Rock could be attributed to more random processes, as indicated by the Kolmogorov-Smirnov testing above. Additionally, weekly offset is probably indicative of the transient nature of the Whale Rock station; species are sampled in the otter trawl either entering or passing through to other estuaries, or exiting the upper bay. Week and temperature preference ranges are also relatively similar to the Fox Island selectivity. Species with a wider or narrower range of preference at Fox Island have a corresponding range span at the Whale Rock. Indeed, a comparison of general preference ranges between the two stations indicates strong spatial correlation for both temperature and week preferences (Fig. 9).

Observed median preference changes could be guided by different mechanisms at the two stations. Additionally, these mechanisms might vary on different temporal scales that allow preferences to converge when averaged over a greater temporal range, 52 years for example.

Cool temperatures and the winter-spring bloom

Species occurring in the winter and early spring months – typically the coldest seasonal temperatures - shifted to later seasonal preferences during the second half of the time series (Fig. 12). Winter-spring blooms diminished in the latter half of the time series but winter and early spring species still increased abundance (e.g., alewife, Atlantic herring, blueback herring, cancer crab). Some of these species might be moving into the mid-bay over time, following the peak annual productivity.

Additionally, winter-spring species' temperature preferences in the first half of the time series might have been within the lower limit of their absolute range, thereby explaining lower abundances as well. When the winter-spring blooms diminished, species shifted towards warmer temperatures to take advantage of the remaining fall bloom, subsequently shifting to warmer thermal preferences and later seasonality. Without survey data from more locations outside of Narragansett Bay, it is difficult to test this hypothesis.

Warm temperatures and the fall bloom

According to the aforementioned zooplankton-grazing hypothesis, chlorophyll concentration declines with warmer temperatures and subsequently increased grazing. Similarly, species with warmer median temperature preferences also declined.

Additionally, species with later week-of-year preference also decreased abundance; this aligned with peak annual chlorophyll concentration occurring on average just a few weeks after peak annual temperatures (Fig. 20). This is counterintuitive given that winter-spring species appeared to increase abundance while shifting preferences to potentially take advantage of the fall bloom. Although the fall bloom persisted in the latter half of the time series, peak chlorophyll concentrations were lower and followed by a more dramatic drop in concentration (Fig. 4b). Edwards and Richardson (2004) demonstrated that the seasonal variations in plankton response generated by climate change might lead to trophic mismatch in marine systems. Fall and early-winter species decline could be associated with declining fall chlorophyll blooms and the more rapid seasonal declines associated with the latter half of the time series (Fig. 4b).

Demersal versus pelagic feeding

Mantel tests of the relationship between chlorophyll concentration and species abundances indicated positive relationships between benthic feeding species and chlorophyll (Table 5). With increased chlorophyll in the water, there could be increased volumes of detritus reaching the benthos and subsequently increased demersal productivity.

Conversely, there may be more pelagic species feeding on zooplankton available in the water column when chlorophyll is heavily grazed. Mantel tests did not reveal significant relationships between pelagic species and chlorophyll to support this theory. Pelagic species are probably not sampled as regularly as demersal species in the GSO trawl which was originally designed to catch demersal species.

Bimodal species and age structure effects

Perhaps in conjunction with the above hypotheses, certain species' life history strategies could alter the results of single parameter quotient analyses. Specifically, some species enter the bay as adults to spawn during specific seasons. Developed juveniles exit the bay to join the adult population at a later time of year. These bimodal species distributions may affect single parameter quotient analyses.

First, the preferences for any time period are a combination of the preferences for juveniles and adults. Consider winter flounder general preferences for week of year (Fig. 8). The wide phenology range encompasses both juvenile and adult distributions. It is also possible that for species with changing age structure, apparent shifts in preference are affected by the altered relative abundances of adults and juveniles. This hypothesis is difficult to test in the data because total biomass measurements began relatively recently, in 1994, and the only species with length data, winter flounder, dates back to just 1985.

Despite the limited temporal range, an ancillary assessment of winter flounder was conducted to explore this hypothesis. Winter flounder catch abundances were compared between 1985-1998 and 1999-2012. The length divide between adults and

juveniles was determined to be about 20cm. Typically adults appear at both stations in the spring, followed by juveniles in the summer (Fig. 21). The general phenologies presented earlier overlap both adult and juvenile seasonal abundances.

At Fox Island, the age structure of the population did not appear to change over time; the relative abundances of adults and juveniles were nearly constant. This would not affect the median preference shifts detected in single parameter quotient analyses. Relative abundances at Whale Rock indicated a changing age structure. In recent years, abundances of adults declined while the abundance of juveniles remained nearly the same (Fig. 21b). Additionally, the first quartile in cumulative proportion of juveniles shifted about two to three weeks later while the median and third quartiles remained the same.

If similar changes in age structure and seasonal distribution occurred in other bimodal species (e.g., alewife, Atlantic herring, blueback herring) since 1961, single parameter quotients could be affected. In future single parameter quotient analyses, species divisions by age structure could reveal different temporal trends in adult and juvenile preferences.

It is important to remember that the temporal range (1985-2012) used for the winter flounder age structure comparison is not comparable to the temporal comparisons made elsewhere in this study (1961-2012). This was merely used to examine the potential for bimodal distributions and changing age structure to affect apparent phenologies and thermal preferences used in this study.

2012: The hottest year

Here, 2012 is compared to the five preceding years (2007 - 2011). Catch distributions shifted earlier in the year at both stations, more so at Whale Rock (Fig. 18). In general, seasonal distribution at Fox Island was more variable. Fox Island, having a shallower water column, changes temperature in response to local atmospheric conditions more readily than the water column at Whale Rock. Whale Rock is probably more influenced by offshore conditions that vary on longer temporal scales. The environmental conditions bringing about warmer temperatures in 2012 might affect fish and invertebrate species at Whale Rock more than Fox Island.

A similar comparison of the warm-water species did not indicate particularly unique differences, as warm-water species abundances are typically much lower than those of dominant species (Table 6; Fig. 19). In 2012, warm-water species seasonal distribution at Whale Rock shifted earlier in the year. Fox Island changed little; differences are hard to decipher due to the low sampling.

Comparisons using just one year are not conclusive and inherently subject to more variation associated with lower sampling abundance. However, it is worth noting that future warming may bring more frequent warm-water species observations and earlier seasonal catch distributions, particularly near the mouth of Narragansett Bay. Current conditions indicate that these warmer-water species do not remain in the bay because the thermal habitat is not persistently suitable; hence, few warm water species observations in the upper bay, near Fox Island. Under future warming scenarios, warm-water species may appear more frequently near Fox Island.

Temporal scale and variability

The relationship between ocean warming and species distributions is further complicated by the fact that this study focused on variation between two 26-year halves of a time series. It is reasonable to assume that the median preference vectors also hide variations occurring on a finer temporal scale. Furthermore, some species whose preference shifts are not directly related to temperature and week variation might be more likely to show interdecadal variation because the true drivers for their preferences might not vary in parallel with temporal changes in bay temperature. Indeed, the degree of interdecadal variation in parameter preference corresponding to the segment metrics (Table 4) indicates that the direction of preference shift at either station is the same for some species throughout the time series and variable for others. It is essentially a cautionary flag for interpreting the apparent changes in parameter preference observed.

However, finer temporal divisions of the survey data also weaken the strength of SPQ analyses. Single parameter quotients lose accuracy at particularly low abundances when each parameter bin is not adequately sampled (Payne 2008). The seemingly large interdecadal variations (Table 4) are likely an artifact of the SPQ analyses' sensitivity to variations in species abundance. This is apparent for species with extremely low abundances in a given time segment. Despite sampling variability concerns, the SPQ metric produces useful insight into changing preferences over the last five decades.

In a regional context

Temporal trends in fish species' abundances, phenologies, and temperature preferences did not reflect direct responses to warming temperatures in Narragansett Bay. Rather, evidence suggests that warming indirectly affects fish distributions by altering the structure of available food in the bay. As evidenced by the metrics and analyses included herein, changes observed over the past five decades are not accounted for exclusively by the approximately 2°C sea surface temperature increase since 1961.

At first, these results even seem to contradict other assessments that establish thermal preferences as a more direct influence on species ranges. A recent paper by Pinksy et al. (2013) indicated that fish and invertebrate species are apt to follow moving climate velocities, or moving isotherms. Their assessment indicated some variation attributable to trophic preferences but maintained physiological thermal limits as the ultimate constraint.

Pinsky et al. (2013) and other more regional assessments of ocean warming and fish distributions might not translate readily to smaller spatial scales as in Narragansett Bay. Rather, this study may provide a ground for exploring local effects of ocean warming of fish distributions. Secondary effects of warming (e.g., primary production) on fish populations are potentially easier to assess using stationary, long-term surveys like the GSO trawl series.

Fish and invertebrate populations in Narragansett Bay could be dictated by a combination of lower ecosystem level processes and finite physiological limits to extreme temperatures. However, the connection between ocean warming, bay production, and species' thermal and seasonal distributions is difficult to establish.

Furthermore, it seems that the effect of lower trophic level impacts also depends on the feeding dynamics and the general temperature and seasonal preferences of the species in question.

Species composition in Narragansett Bay changed several times in the past (Collie et al. 2008; Jeffries and Terceiro 1985), historically corresponding with changing fisheries (Oviatt et al. 2003). Understanding the mechanisms behind these changes (e.g., ocean warming) and resolving issues of local variability and temporal scale will help to develop appropriate management strategies for fisheries.

Table1. Two-sample Kolmogorov-Smirnov test p values and observed maximum distances between weighted cumulative distributions of abundances by sea surface temperature (SST) and weeks (1961-1986 versus 1987-2012) (alpha=0.05). First column of each station and parameter corresponds to p-values, second column is the maximum distance between distributions. Warmer temperature preferences and earlier phenologies in the latter half of the time series are indicated by '+'; cooler temperature preferences and later phenologies are indicated by '-'. Insignificant relationships are denoted by smaller, italicized text.

	Fox Island				Whale Rock			
Species	*SST*		*Weeks*		*SST*		*Weeks*	
Alewife	*0.054*	*+0.518*	0.026	+ 0.648	0.048	– 0.31	*0.286*	*– 0.229*
Atlantic herring	*0.156*	*+0.48*	*0.536*	*+ 0.362*	*0.525*	*+ 0.147*	*0.348*	*– 0.192*
Blueback herring	*0.924*	*–0.212*	*0.293*	*+ 0.508*	0.038	– 0.377	*0.062*	*+ 0.321*
Butterfish	0.014	+0.276	*0.116*	*+ 0.269*	0.002	+ 0.236	0.03	– 0.22
Cancer crab	<0.001	+0.434	<0.001	+ 0.423	*0.546*	*+ 0.054*	*0.464*	*– 0.065*
Conch	*0.822*	*–0.047*	*0.782*	*– 0.043*	*0.197*	*+ 0.537*	*0.724*	*+ 0.445*
Fourspot flounder	0.042	+0.251	<0.001	– 0.64	*0.484*	*+ 0.095*	*0.424*	*– 0.076*
Grubby & Shorthorn sculpin	*0.056*	*+0.23*	*0.413*	*– 0.116*	*0.591*	*– 0.806*	*0.741*	*– 0.75*
Horseshoe crab	<0.001	–0.311	<0.001	+ 0.231	*0.108*	*+ 0.183*	*0.97*	*+ 0.064*
Little skate	*0.148*	*+0.11*	<0.001	+ 0.226	*0.245*	*– 0.079*	*0.626*	*+ 0.048*
Lobster	*0.556*	*+0.063*	*0.896*	*+ 0.044*	*0.206*	*+ 0.102*	<0.001	– 0.279
Long finned squid	<0.001	+0.269	<0.001	+ 0.41	*0.306*	*+ 0.11*	*0.886*	*– 0.05*
Longhorned sculpin	<0.001	+0.55	<0.001	– 0.581	*0.972*	*– 0.084*	*0.129*	*+ 0.225*
Northern kingfish	*0.344*	*+0.151*	*0.552*	*– 0.162*	*0.254*	*+ 0.307*	*0.29*	*– 0.258*
Northern searobin	*0.15*	*+0.158*	*0.396*	*– 0.127*	0.001	– 0.266	0.001	– 0.303
Red hake	*0.934*	*+0.097*	*0.99*	*– 0.076*	*0.338*	*+ 0.178*	*0.269*	*– 0.252*
Scup	0.003	+0.19	<0.001	+ 0.325	*0.731*	*+ 0.079*	*0.494*	*+ 0.11*
Silver hake	*0.708*	*–0.122*	*0.504*	*+ 0.142*	*0.177*	*– 0.116*	*0.583*	*– 0.081*
Smooth dogfish	0.007	+0.352	*0.379*	*+ 0.152*	*0.548*	*+ 0.121*	*0.529*	*+ 0.138*
Spider crab	*0.236*	*+0.144*	0.014	+ 0.218	*0.367*	*+ 0.167*	*0.28*	*+ 0.165*
Summer flounder	*0.202*	*–0.087*	0.016	+ 0.108	<0.001	+ 0.307	<0.001	– 0.223
Tautog	*0.524*	*+0.076*	*0.248*	*– 0.109*	*0.679*	*+ 0.205*	*0.873*	*+ 0.192*
Weakfish	*0.934*	*–0.119*	*0.888*	*+ 0.128*	*0.62*	*– 0.186*	*0.884*	*+ 0.118*
Windowpane flounder	<0.001	+0.326	<0.001	+ 0.25	*0.172*	*– 0.135*	*0.25*	*+ 0.156*
Winter flounder	<0.001	+0.194	0.013	+ 0.122	0.006	– 0.131	0.018	– 0.115

Table 2. Sample sizes for 1961-1986 (N_1) and 1987-2012 (N_2). Species numbers correspond to Figure 7; colors correspond to species type (pelagic=blue, demersal=pink, invertebrate=purple, squid=green).

		Fox Island		Whale Rock	
	Species	N_1	N_2	N_1	N_2
1	Alewife	88	7525	564	4287
2	Atlantic herring	2136	11282	2735	10003
3	Blueback herring	291	1762	1001	551
4	Butterfish	8960	71631	23682	161706
5	Cancer crab	22699	96981	60432	115482
6	Conch	5914	8042	37	117
7	Fourspot flounder	500	754	4058	15061
8	Grubby & Shorthorn sculpin	1050	138	375	16
9	Horseshoe crab	4456	513	121	110
10	Little skate	2162	4841	8676	55501
11	Lobster	2513	27764	13692	20749
12	Long finned squid	8476	37033	14401	90182
13	Longhorned sculpin	3158	196	10076	2627
14	Northern kingfish	135	230	190	290
15	Northern searobin	13734	784	2672	2711
16	Red hake	676	902	30170	4106
17	Scup	119872	219579	18756	57673
18	Silver hake	4971	2481	65870	23972
19	Smooth dogfish	547	165	318	95
20	Spider crab	10431	17308	1269	3119
21	Summer flounder	2042	4306	576	5173
22	Tautog	2732	475	90	82
23	Weakfish	675	1762	204	1017
24	Windowpane flounder	17786	3435	12838	14133
25	Winter flounder	178546	33244	40875	29946

Table 3. Preference selectivity metrics for temperature (D_t) and week (D_w) at the Fox Island and Whale Rock stations. Metrics greater than 1 indicate a wider range of selectivity between in 1987-2012; metrics less than 1 indicate a narrower range of selectivity in 1987-2012. Gray, italic fonts indicate distributions that were not significantly different across the time series (Table 1).

	Fox Island		Whale Rock	
Species	D_t	D_w	D_t	D_w
Alewife	*1.09*	2.1	0.7	*1.22*
Atlantic herring	*0.57*	*3.58*	*1.19*	*1.55*
Blueback herring	*3.52*	*0.7*	0.56	*2.27*
Butterfish	1.39	*0.7*	1.08	1.05
Cancer crab	2.67	4.88	*0.94*	*1.09*
Conch	*1.14*	*0.99*	*0.59*	*0.56*
Fourspot flounder	0.84	0.42	*1.27*	*0.88*
Grubby & Shorthorn sculpin	*1.25*	*1.13*	*8.5*	*5.77*
Horseshoe crab	0.96	1.23	*1.27*	*1.12*
Little skate	*0.94*	2.34	*1.16*	*1.11*
Lobster	*0.97*	*1.01*	*1.09*	0.81
Long finned squid	0.94	1.03	*1.02*	*0.9*
Longhorned sculpin	2.99	2.01	*0.85*	*0.6*
Northern kingfish	*0.72*	*0.68*	*1.64*	*1.54*
Northern searobin	*1.77*	*1.36*	0.5	0.39
Red hake	*1.14*	*0.9*	*1.78*	*1.82*
Scup	1.07	1.63	*1.28*	*1.14*
Silver hake	*1.11*	*0.43*	*0.94*	*1.15*
Smooth dogfish	0.41	*1.15*	*1.72*	*1*
Spider crab	*1.81*	1.58	*3.03*	*0.93*
Summer flounder	*1.47*	1.21	1.58	0.73
Tautog	*1.14*	*0.92*	*2.44*	*1.23*
Weakfish	*1.06*	*0.95*	*0.87*	*1.15*
Windowpane flounder	0.65	0.76	*1.03*	*1.43*
Winter flounder	1	0.78	1.11	0.87

Table 4. Total abundance (N) and interdecadal variation metrics for temperature (M_t) and week (M_w) preference at Fox Island and Whale Rock stations. Metrics greater than one indicate more variability. Metrics equal to one indicate that the net variation between the four segments was equal to the variation between the first and fourth segments. Gray italic fonts correspond to distributions that were not significantly different across the time series (Table 1).

	Fox Island			Whale Rock		
Species	N	M_t	M_w	N	M_t	M_w
Alewife	7613	1.23	10.45	4851	*1*	*1.84*
Atlantic herring	13418	*2.36*	*80.37*	12738	*1.2*	*18.14*
Blueback herring	2053	*1.84*	*1.04*	1552	*1.43*	*3.31*
Butterfish	80591	3.36	*1*	185388	3.79	25.67
Cancer crab	119680	2.08	1.39	175914	*1.96*	*1.48*
Conch	13956	*2.1*	*1.17*	154	*4.63*	*6.95*
Fourspot flounder	1254	2.77	1.21	19118	*1.17*	*1.85*
Grubby & Shorthorn sculpin	1188	*1.15*	*6.08*	391	*1.94*	*1.15*
Horseshoe crab	4970	1.73	4.09	231	*1.88*	*2.73*
Little skate	7003	*1.18*	1	64177	*3.56*	*1.97*
Lobster	30277	*1.48*	*2.85*	34441	3.08	1.24
Long finned squid	45509	1.47	1.63	104583	*3.9*	*4.47*
Longhorned sculpin	3354	4.87	1	12703	*4.37*	*1*
Northern kingfish	365	*146.23*	*3.62*	480	*4.94*	*4.87*
Northern searobin	14518	*6.17*	*13.85*	5383	1	1.1
Red hake	1578	*2.01*	*2.15*	34276	*1.33*	*1.15*
Scup	339451	1	2.27	76428	*10.19*	*5.78*
Silver hake	7452	*1.35*	*1*	89842	*2.45*	*1.36*
Smooth dogfish	712	38	*4.3*	413	*1*	*4.18*
Spider crab	27739	*23.71*	1.83	4388	*14.34*	*89.76*
Summer flounder	6348	*4.83*	8.46	5749	1.39	14.39
Tautog	3207	*4.53*	*4.89*	172	*13.34*	*68.5*
Weakfish	2437	*9.75*	*11.15*	1221	*3.78*	*3.88*
Windowpane flounder	21221	1	6.86	26972	*80.58*	*65.16*
Winter flounder	211790	1	1	70821	97.52	3.53

Table 5. Significance values and statistics from mantel test of chlorophyll concentration and species abundance (Fox Island and Whale Rock) by week and year. Fox Island species are compared with the Fox Island chlorophyll time series. Whale Rock species are compared with the GSO dock chlorophyll time series.

	Fox Island		Whale Rock	
Species	***p***	***r***	***p***	***r***
Alewife	*0.811*	*−0.137*	*0.856*	*−0.148*
Atlantic herring	*0.973*	*−0.212*	*0.25*	*0.089*
Blueback herring	*0.927*	*−0.204*	0.022	0.34
Butterfish	*0.941*	*−0.229*	*0.949*	*−0.2*
Cancer crab	*0.626*	*−0.075*	*0.312*	*0.06*
Conch	*0.386*	*0.018*	*0.584*	*−0.04*
Fourspot flounder	*0.371*	*0.027*	*0.546*	*−0.034*
Grubby & Shorthorn sculpin	0.01	0.196	0.034	0.146
Horseshoe crab	0.029	0.308	*0.057*	*0.127*
Little skate	*0.052*	*0.285*	0.035	0.261
Lobster	*0.77*	*−0.113*	*0.903*	*−0.167*
Long finned squid	*0.879*	*−0.166*	*0.934*	*−0.183*
Longhorned sculpin	*0.492*	*−0.024*	*0.725*	*−0.101*
Northern kingfish	*0.472*	*0*	*0.294*	*0.04*
Northern searobin	*0.182*	*0.138*	*0.091*	*0.227*
Red hake	*0.323*	*0.051*	*0.952*	*−0.22*
Scup	*0.303*	*0.07*	*0.23*	*0.092*
Silver hake	*0.131*	*0.18*	*0.388*	*0.027*
Smooth dogfish	*0.514*	*−0.025*	*0.243*	*0.071*
Spider crab	*0.636*	*−0.067*	*0.917*	*−0.193*
Summer flounder	*0.717*	*−0.091*	*0.174*	*0.139*
Tautog	*0.128*	*0.164*	0.021	0.155
Weakfish	*0.704*	*−0.11*	*0.937*	*−0.183*
Windowpane flounder	0.044	0.278	*0.786*	*−0.118*
Winter flounder	0.044	0.298	*0.843*	*−0.134*

Table 6. Warm water species list.

Common name	Scientific name
Atlantic bonito	*Sarda sarda*
Atlantic moonfish	*Selene setapinnis*
Bigeye	*Priacanthus arenatus*
Bigeye scad	*Selar crumenophthalmus*
Blue runner	*Caranx crysos*
Bluespotted cornetfish	*Fistularia tabacaria*
Cero	*Scomberomorus regalis*
Clearnose skate	*Raja eglanteria*
Cow−nosed ray	*Rhinoptera bonasus*
Crevalle	*Caranx hippos*
Dwarf goatfish	*Upeneus parvus*
Flying gurnard	*Dactylopterus volitans*
French grunt	*Haemulon flavolineatum*
Fringed filefish	*Monacanthus ciliatus*
Glasseye snapper	*Priacanthus cruentatus*
Grey triggerfish	*Balistes capriscus*
Guaguanche	*Sphyraena guachancho*
King mackerel	*Scomberomorus cavalla*
lined seahorse	*Hippocampus erectus*
Lookdown	*Selene vomer*
Mackeral scad	*Decapterus macarellus*
Mahogany snapper	*Lutjanus mahogoni*
Northern puffer	*Sphoeroides maculatus*
Northern Sennet	*Sphyraena borealis*
Orange filefish	*Aluterus schoepfii*
Penaeus shrimp	*Penaeus sp.*
Planehead filefish	*Stephanolepis hispidus*
Roughtail sting ray	*Dasyatis centroura*
Sargassumfish	*Histrio histrio*
Saurel	*Trachurus trachurus*
Shame faced crab	*Calappa flammea*
Sheepshead	*Archosargus probatocephalus*
Short Bigeye	*Pristigenys alta*
Spiny butterfly ray	*Gymnura altavela*
Spot	*Leiostomus xanthurus*
Spotted goatfish	*Pseudupeneus maculatus*
striped burrfish	*Chilomycterus schoepfii*
Striped mullet	*Mugil cephalus*

Table 7. Summary table of species traits. Migratory species are indicated by Xs. Directions of thermal preference and phenology shifts in the latter half of the time series are indicated by 'warmer', 'cooler', 'later', and 'earlier.' Species with insignificant shifts in distribution (Appendix A-2) are not indicated. Directions of significant abundance regression (Appendix A-3) are indicated by '+' or '-'.

				Fox Island			Whale Rock		
	Species	Migratory	Habitat	*SST, Week, Abundance*			*SST, Week, Abundance*		
1	Alewife	X	Pelagic		Later	+	Cooler		+
2	Atlantic herring	X	Pelagic						
3	Blueback herring	X	Pelagic				Cooler		−
4	Butterfish	X	Pelagic	Warmer		+	Warmer	Earlier	+
5	Cancer crab		Invertebrate	Warmer	Later	+			+
6	Conch		Invertebrate			+			
7	Fourspot flounder	X	Demersal	Warmer	Earlier	+			
8	Grubby & Shorthorn sculpin	X	Demersal			−			
9	Horseshoe crab	X	Invertebrate	Cooler	Later	−			
10	Little skate	X	Demersal		Later	+			
11	Lobster	X	Invertebrate			+		Earlier	
12	Long finned squid	X	Squid	Warmer	Later	+			
13	Longhorned sculpin	X	Demersal	Warmer	Earlier	−			
14	Northern kingfish	X	Demersal						
15	Northern searobin	X	Demersal			−	Cooler	Earlier	
16	Red hake	X	Demersal						−
17	Scup	X	Demersal	Warmer	Later	+			+
18	Silver hake	X	Demersal			−			−
19	Smooth dogfish	X	Demersal	Warmer		−			−
20	Spider crab		Invertebrate		Later	+			+
21	Summer flounder	X	Demersal		Later	+	Warmer	Earlier	+
22	Tautog	X	Demersal			−			
23	Weakfish	X	Pelagic						+
24	Windowpane flounder	X	Demersal	Warmer	Later	−			−
25	Winter flounder	X	Demersal	Warmer	Later	−	Cooler	Earlier	−

Figure 1. Temperature and week sampling distributions at Fox Island (a) and Whale Rock (b) for 1961-1986 (black) and 1987-2012 (red).

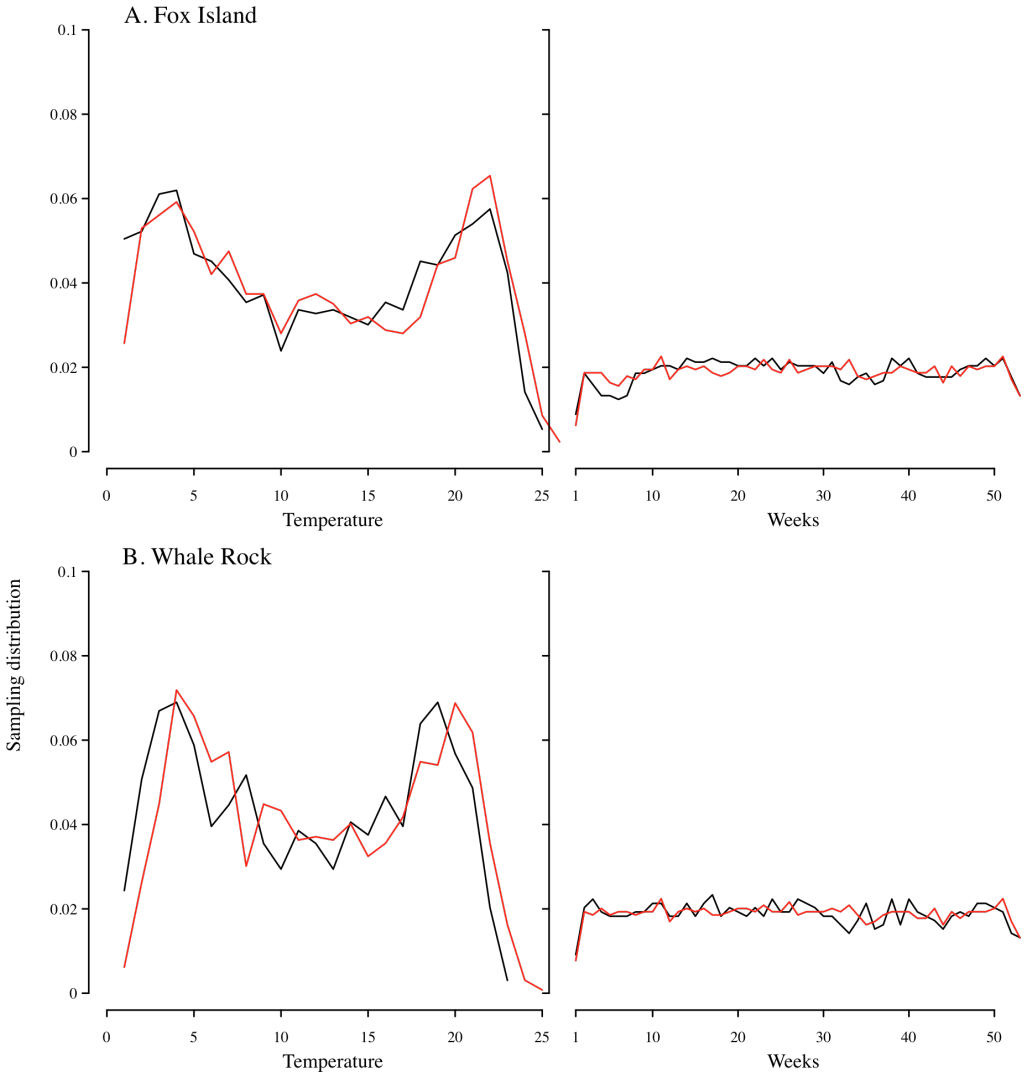


Figure 2. Temporal trends in seasonal temperatures at Fox Island (black) and Whale Rock (red) with fitted smooth splines (df=5). Seasons are defined by months: winter (January, February, March), spring (April, May, June), summer (July, August, September), fall (October, November, December).

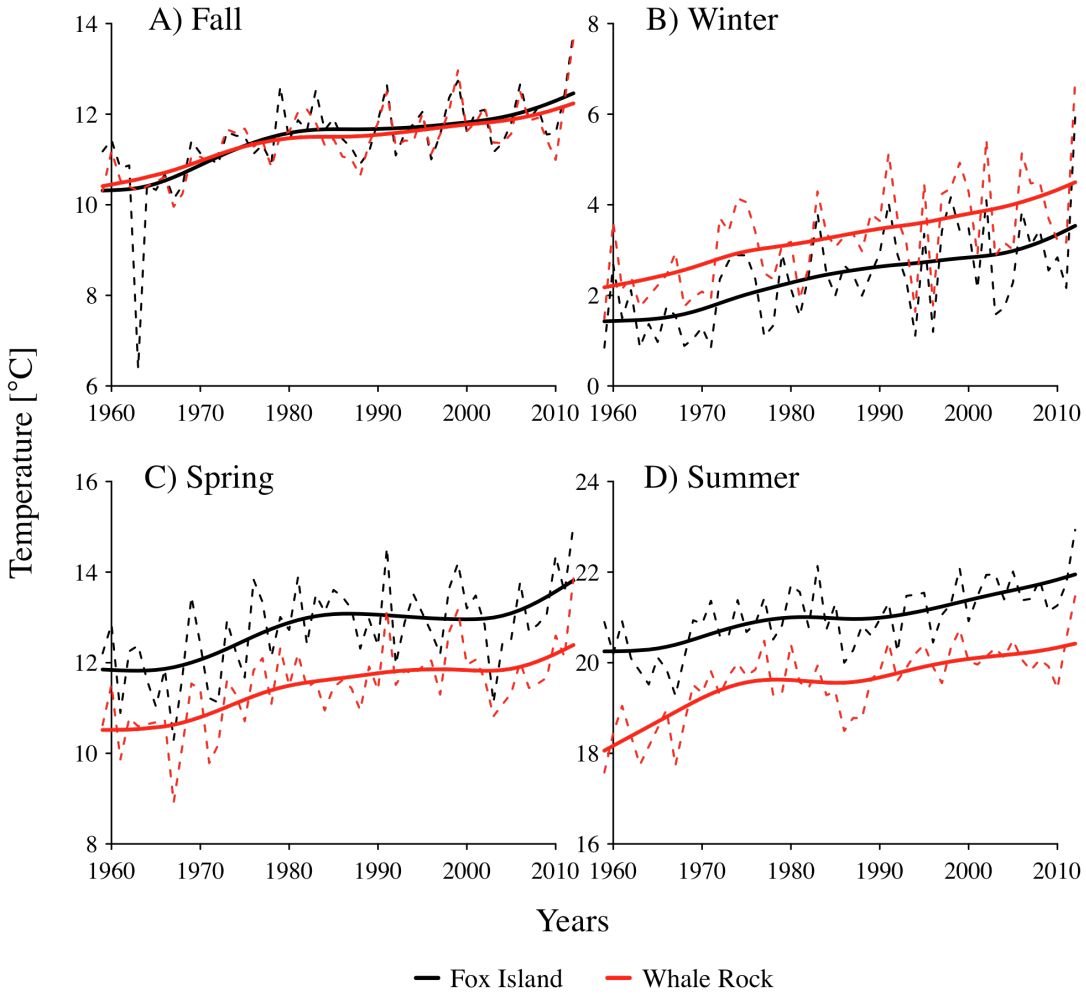


Figure 3. Mean weekly sea surface temperatures (dotted) at Fox Island (a, b) and Whale Rock (c, d) stations; fitted with smooth splines (solid; df=7). Time series divided into 13-year (a, c) and 26-year (b, d) segments.

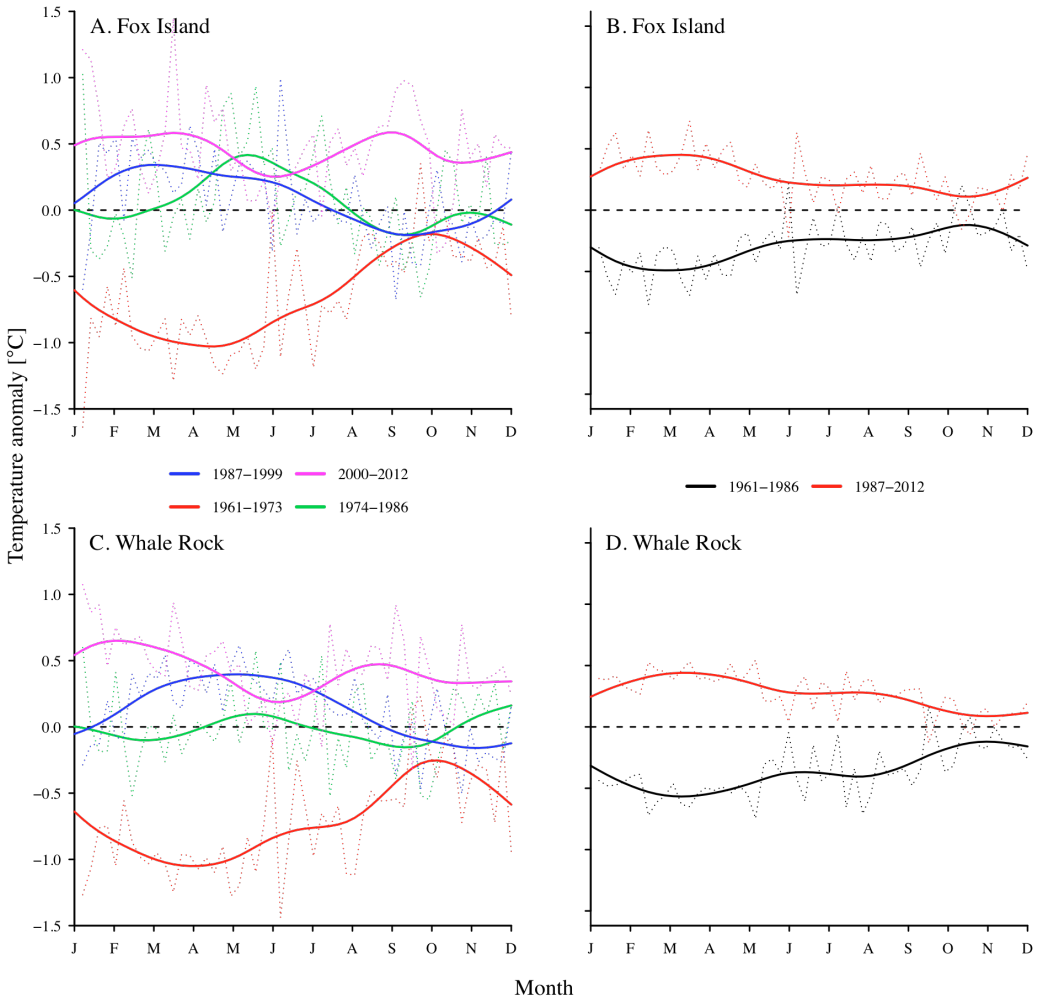


Figure 4. Temporal trends in Chlorophyll a (µg L^{-1}) in Narragansett Bay, Rhode Island, USA. (a) Mean yearly concentrations from the mid-bay station (solid) 1973-1996 and 1999-2011 and the GSO dock (dashed) 1977-2011. (b) Weekly mean concentrations (dotted) from the mid-bay station, Fox Island, with fitted smooth splines (solid). (c) Weekly mean concentrations (dotted) from the GSO dock fitted with smooth splines (solid).

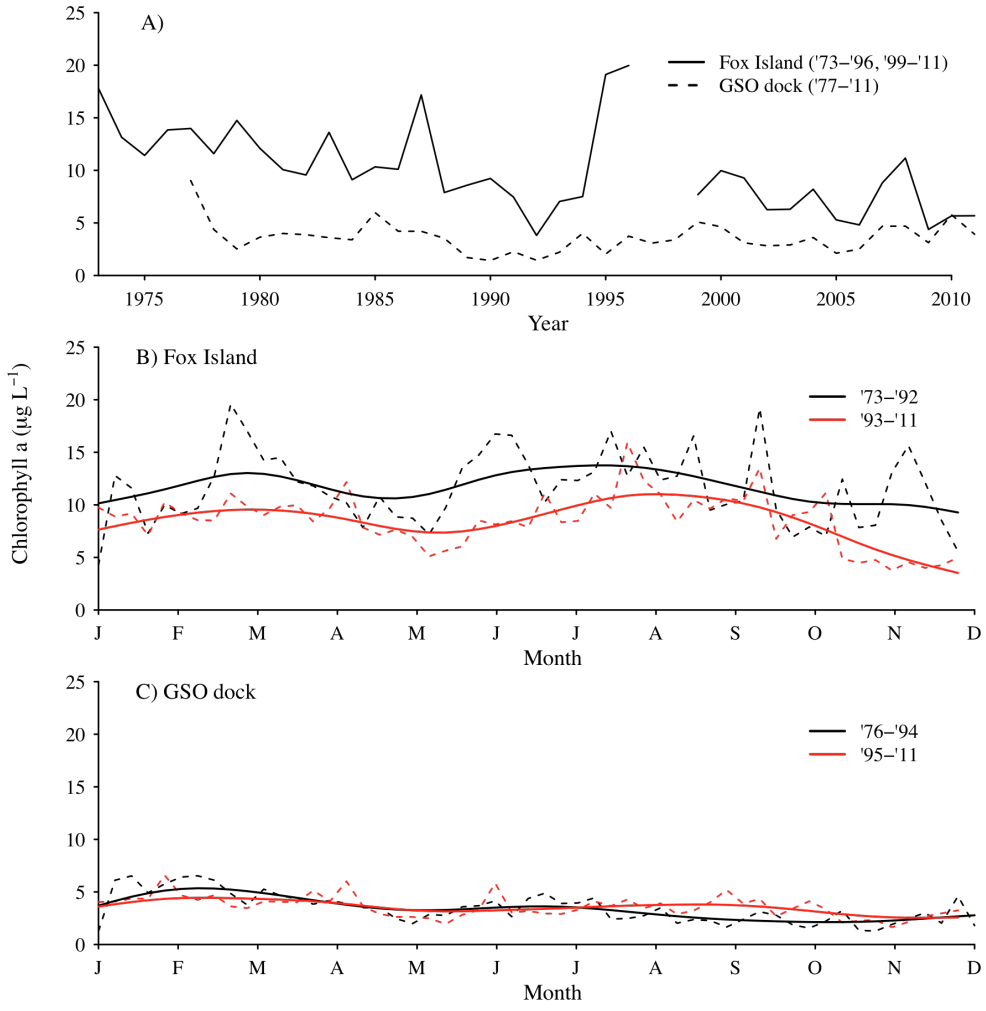


Figure 5. Regression analysis of annual and seasonal means chlorophyll a (µg/L) in the upper bay. Annual, fall and winter mean chlorophyll a concentrations have declined significantly.

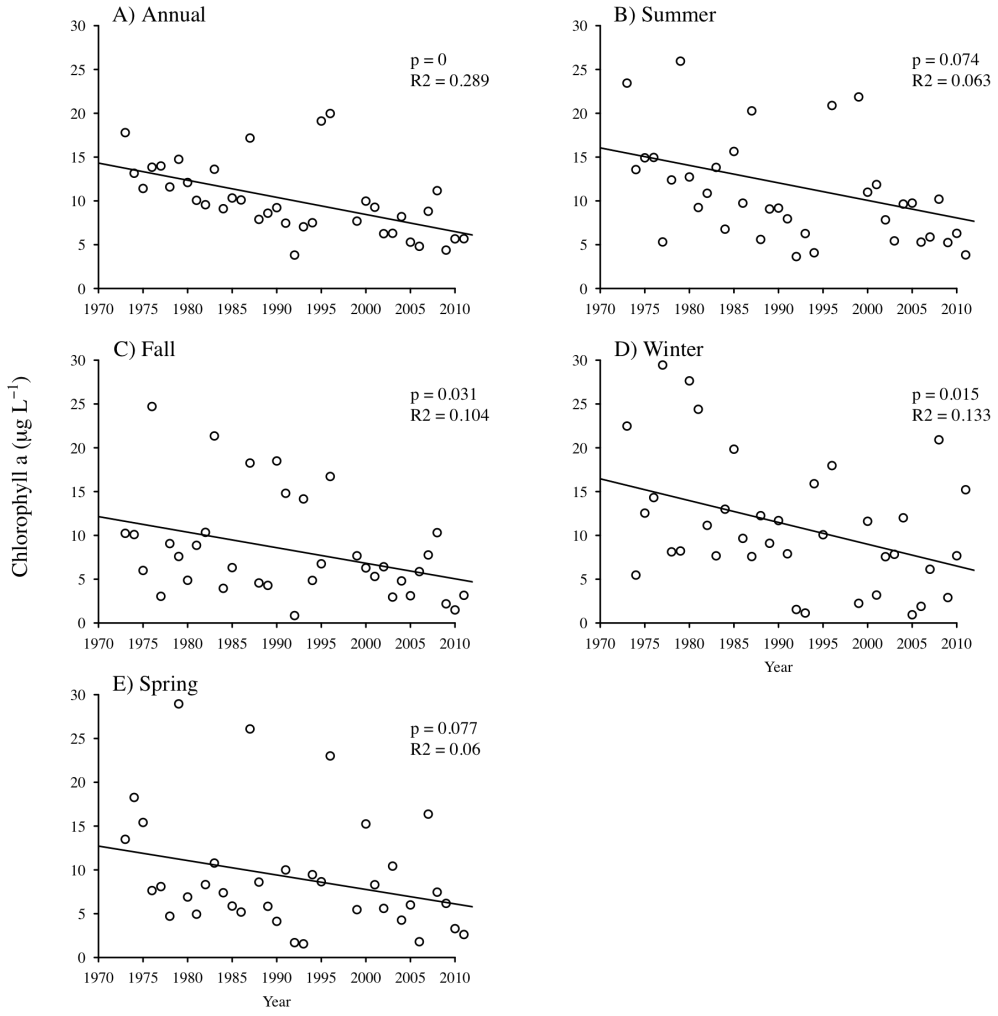


Figure 6. Regression analysis of annual and seasonal means chlorophyll a (µg/L) from the GSO dock station. No significant trends in annual or seasonal means occurred.

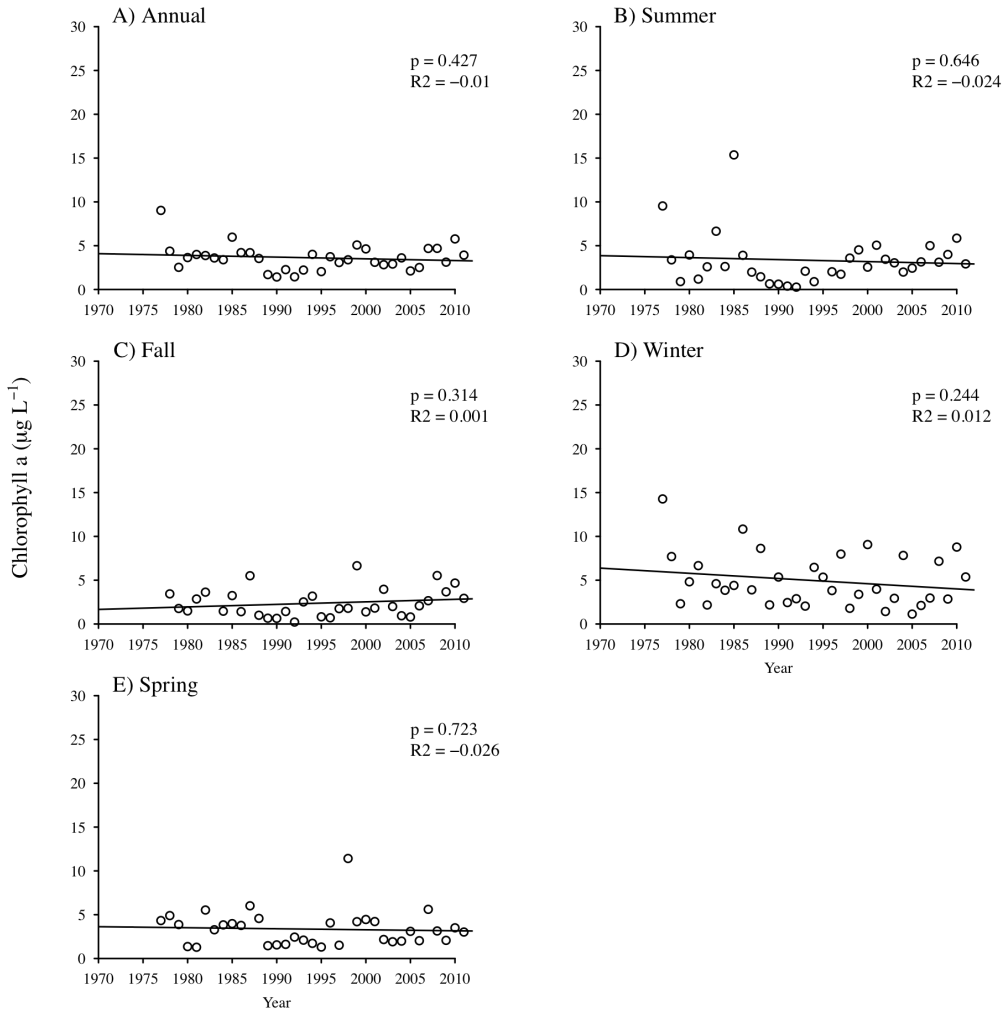


Figure 7. Top 25 species weekly mean catch per tow abundances at Fox Island (a), Whale Rock (b) and weekly cumulative proportion of yearly abundances at Fox Island (c), Whale Rock (d).

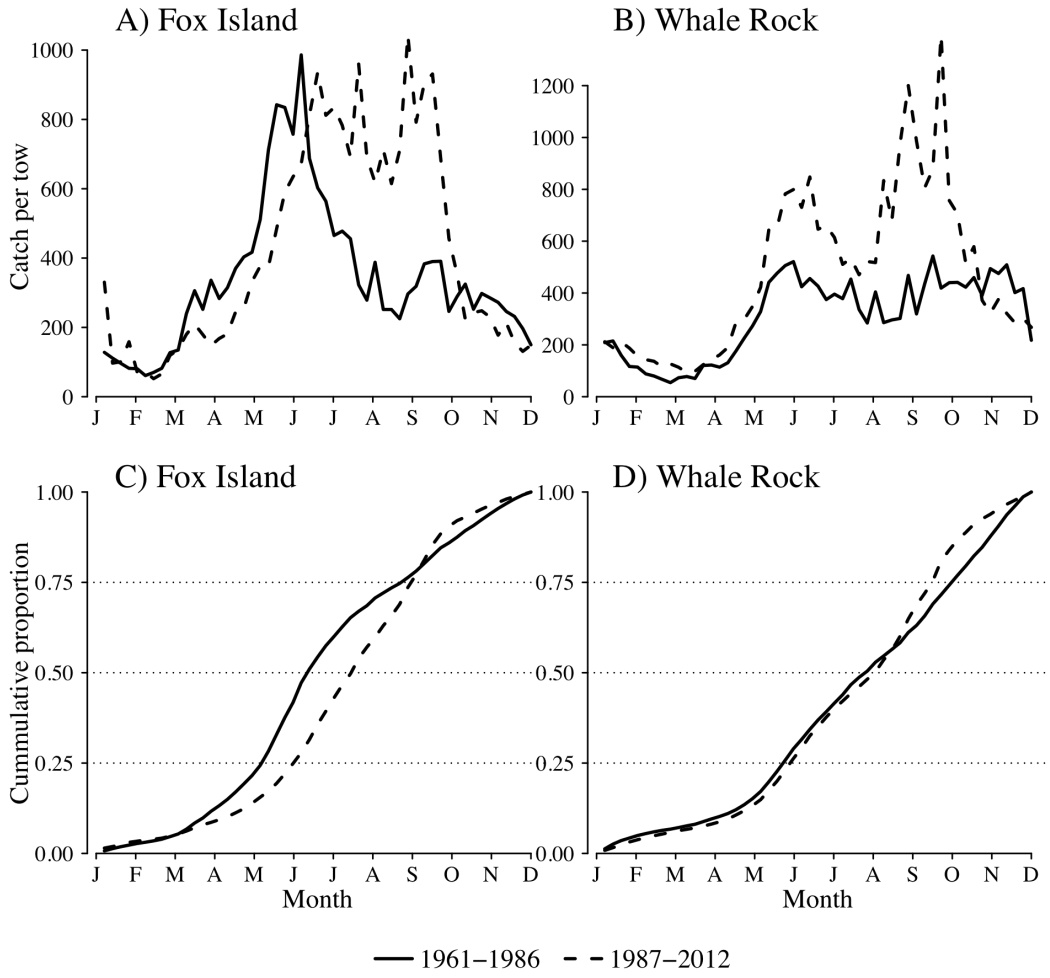
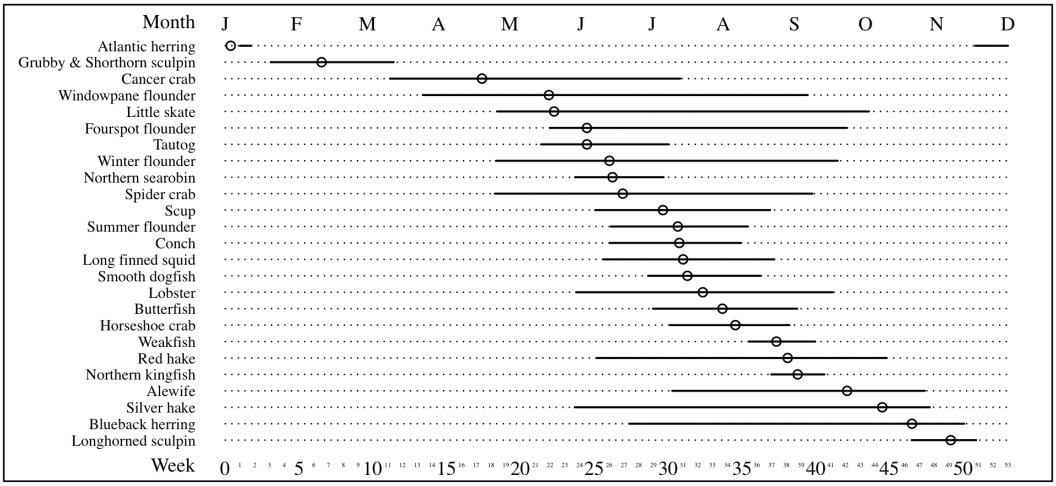


Figure 8. Selectivity (solid line; 25th-75th percentiles) and median (circle) preferences for week (1961-2012) for the top 25 species Fox Island (a) and Whale Rock (b) stations. Week of year along the bottom axes.

A. Fox Island



B. Whale Rock

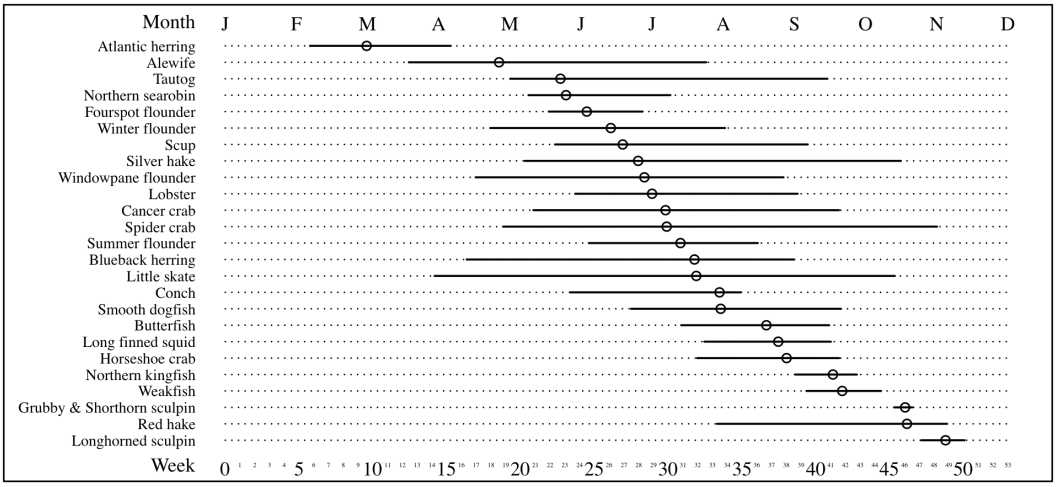


Figure 9. Spatial correlation comparison of general preferences ranges (25th to 75 percentile) and median preference (red circles) between Fox Island and Whale Rock for temperature (a) and week of year (b).

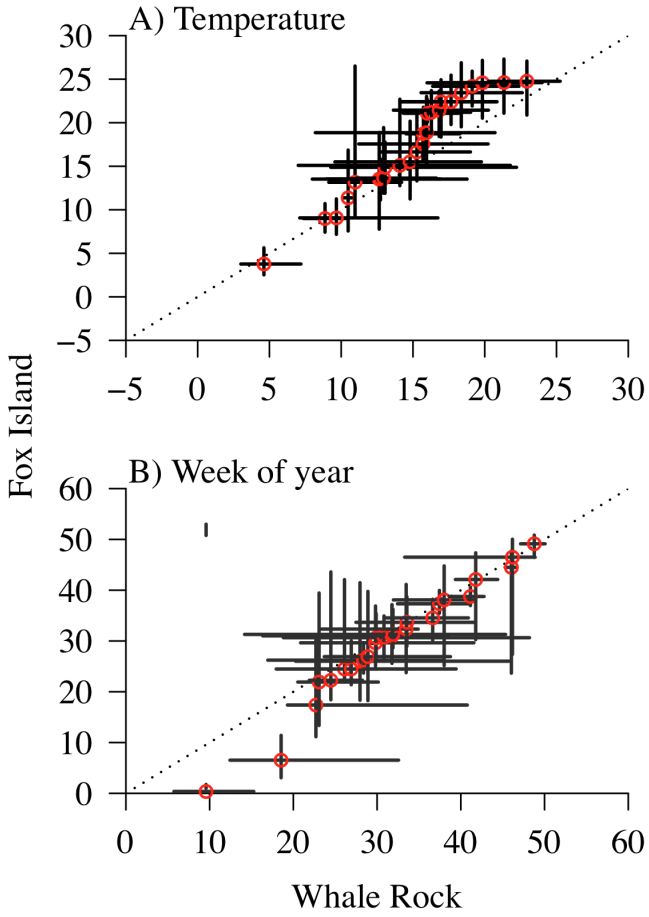
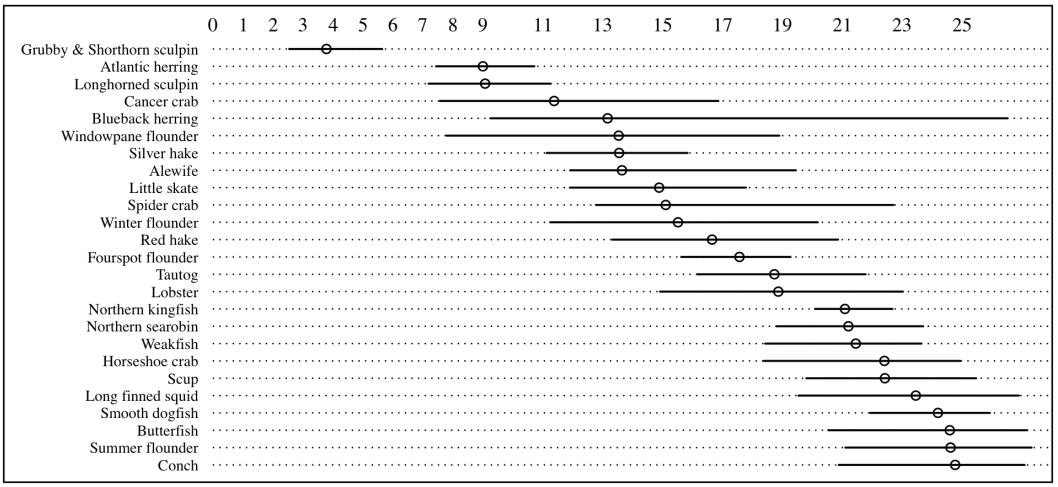


Figure 10. Selectivity (solid line; 25th-75th percentiles) and median (circle) preferences for temperature (1961-2012) for the top 25 species Fox Island (a) and Whale Rock (b) stations. Temperature in degrees Celsius along the x-axis.

A. Fox Island



B. Whale Rock

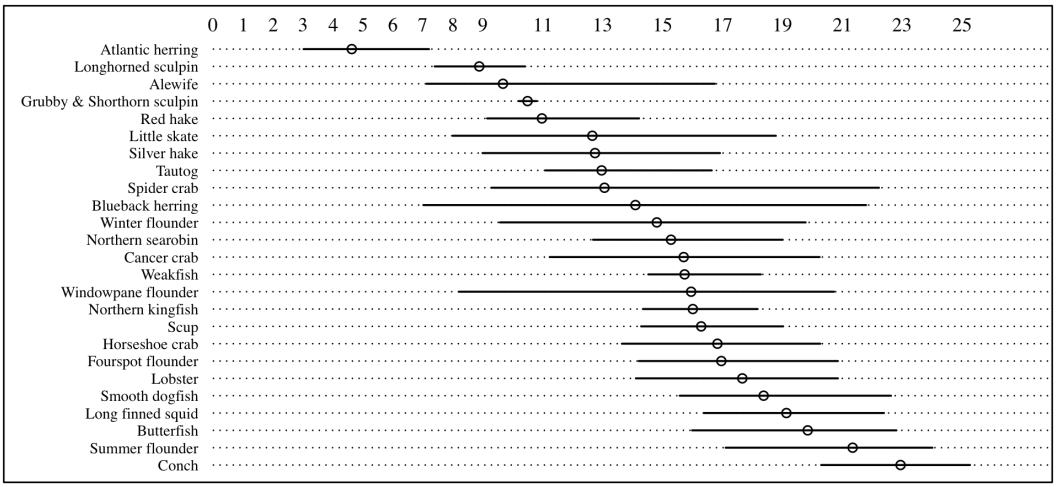


Figure 11. Median parameter preferences of species with fixed single parameter preferences for both halves of the time series (1961-1986 and 1987-2012) plotted as vectors pointed in the direction of preference shift. Weekly mean temperatures for 1961-1986 (dark grey) and 1987-2012 (light grey) indicate the seasonal temperature distributions at Fox Island (a) and Whale Rock (b). Fixed week preference vectors are vertical; fixed temperature preference vectors are horizontal.

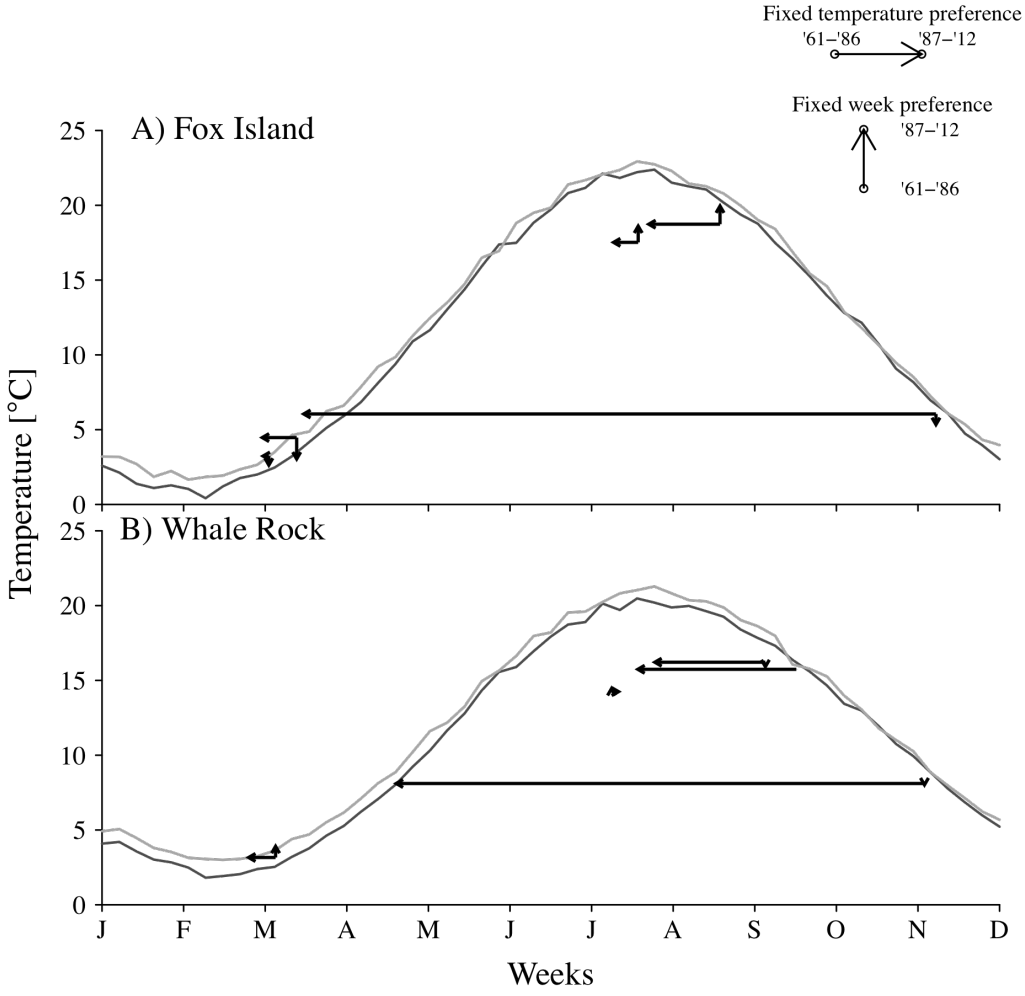


Figure 12. Observed median parameter preferences for both halves of the time series (1961-1986 and 1987-2012) plotted as vectors pointed in the direction of preference shift. Weekly mean temperatures for 1961-1986 (dark grey) and 1987-2012 (light grey) indicate the seasonal temperature distributions at Fox Island (a) and Whale Rock (b). Line type and widths correspond to annual abundance regressions (Fig. 16; Fig. 17). Black vectors correspond to species whose species distributions for temperature and weeks were not significant (Table 1). Line type key refers to regression slopes (Fig. A-6; Fig. A-7). Species numbers are listed in Table 2.

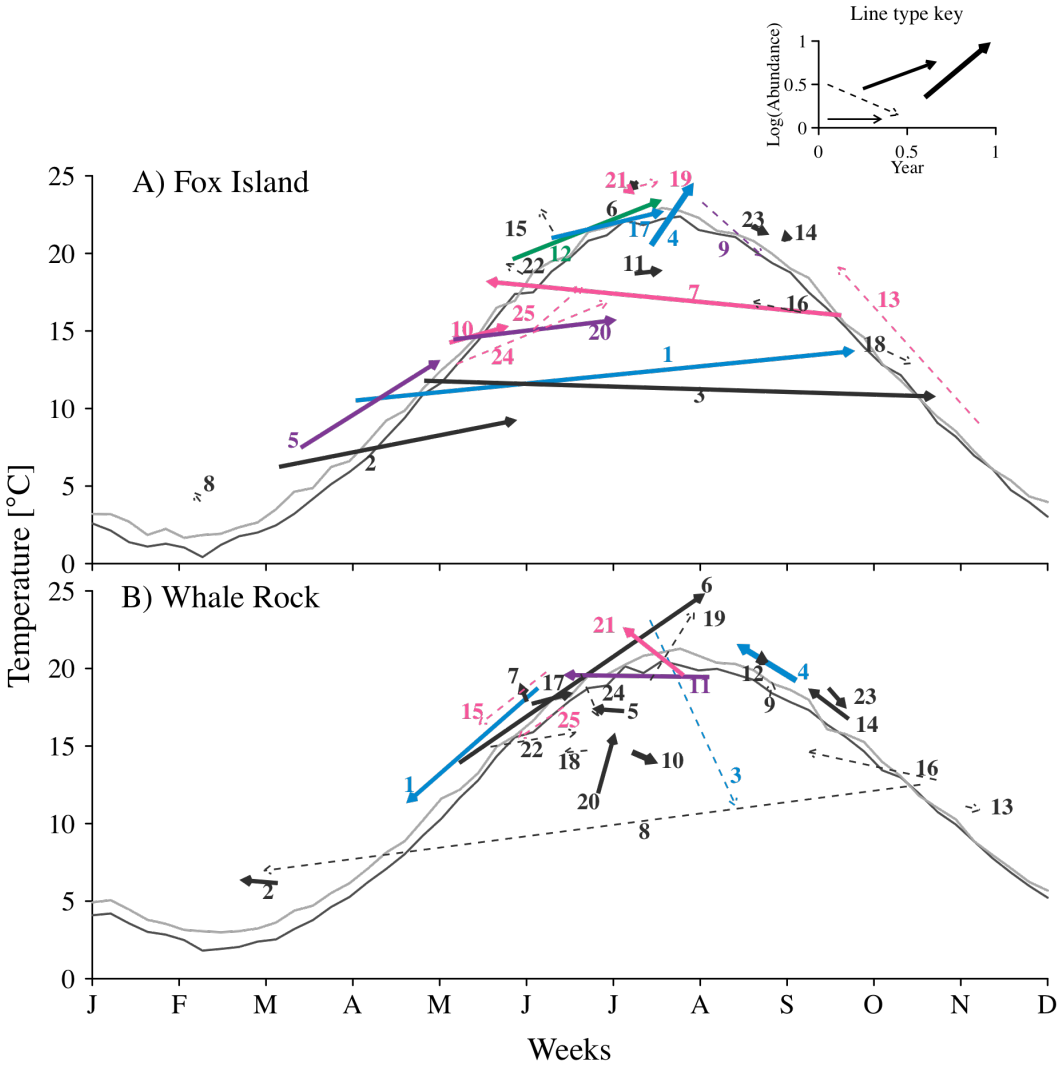


Figure 13. Spatial correlation comparison of median preference shifts - or, the differences between median preferences of the first and second halves of the time series- between Fox Island and Whale Rock for temperature (a) and week of year (b).

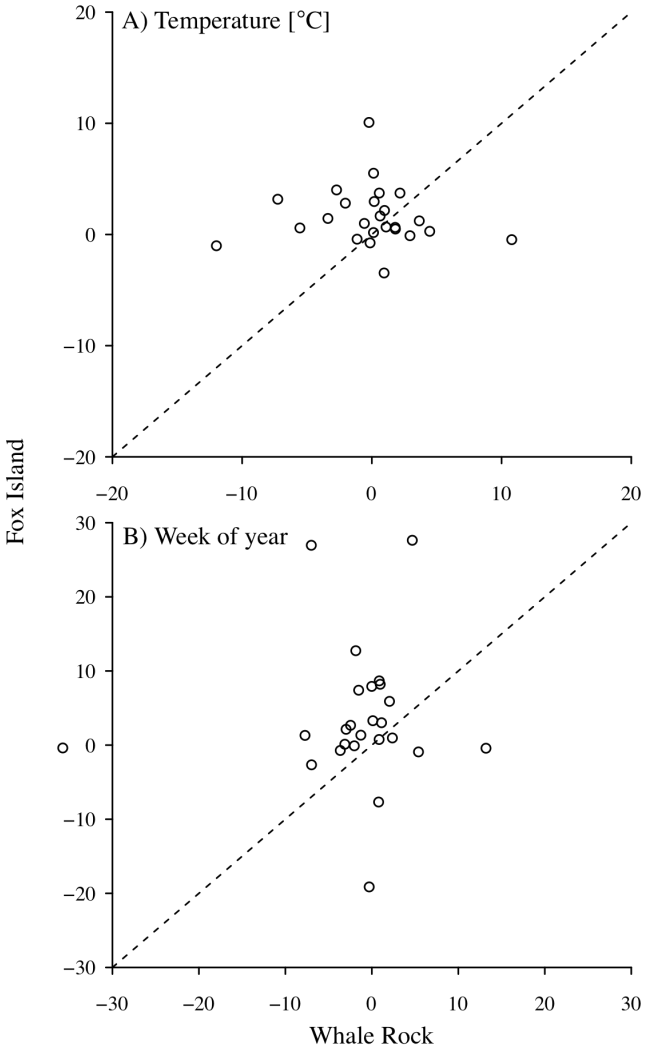


Figure 14. A comparison of species' rate of abundance change versus median temperature (1961-2012). Rate of abundance change is derived from the slope of abundance regressions (Appendix A-3). Species with no significant regression are denoted by 'X's.

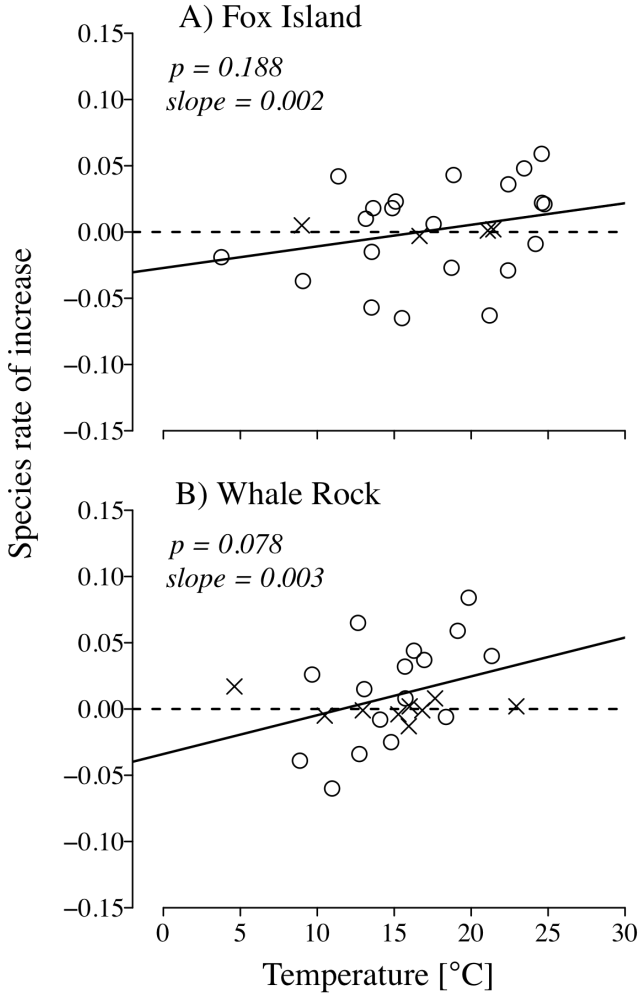


Figure 15. Species rate of change versus change in temperature and week of year preferences across the two halves of the time series (1961-1986, 1987-2012). There does not appear to be a relationship at either station. Species with no significant regression are denoted by 'X's.

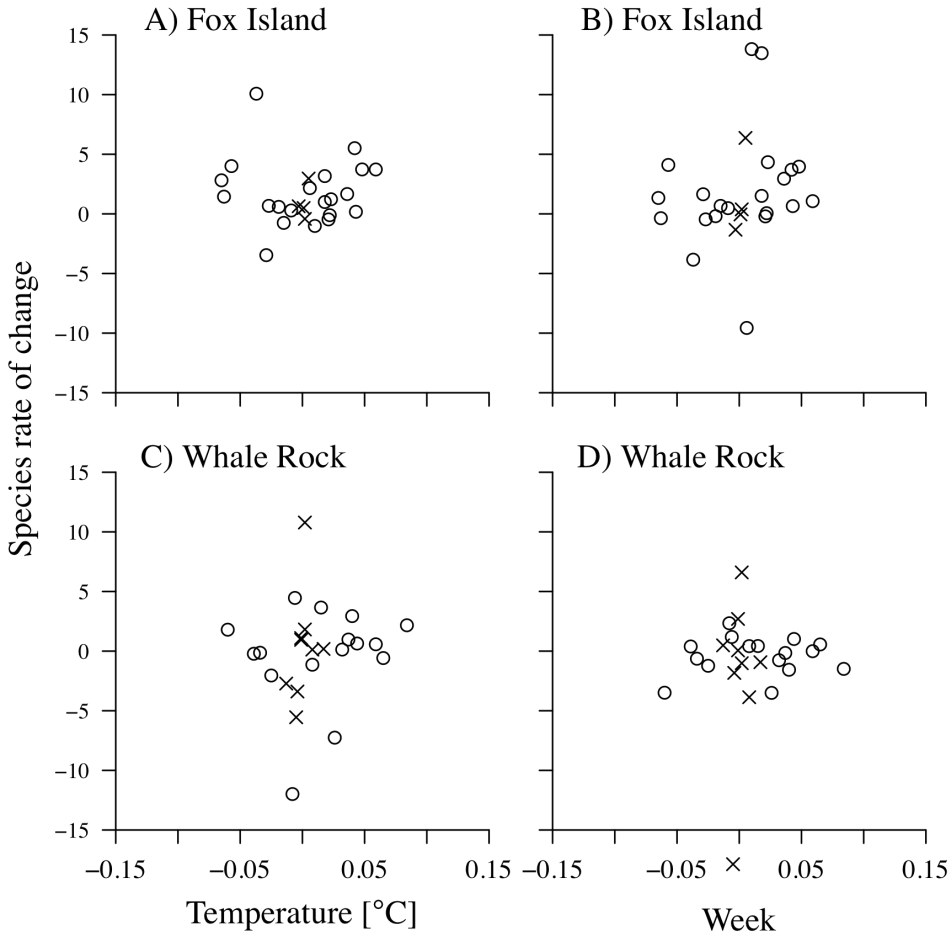


Figure 16. Mean weekly sea surface temperatures from 1961-2011 (solid) and 2012 (dashed) at Fox Island (a) and Whale Rock (b).

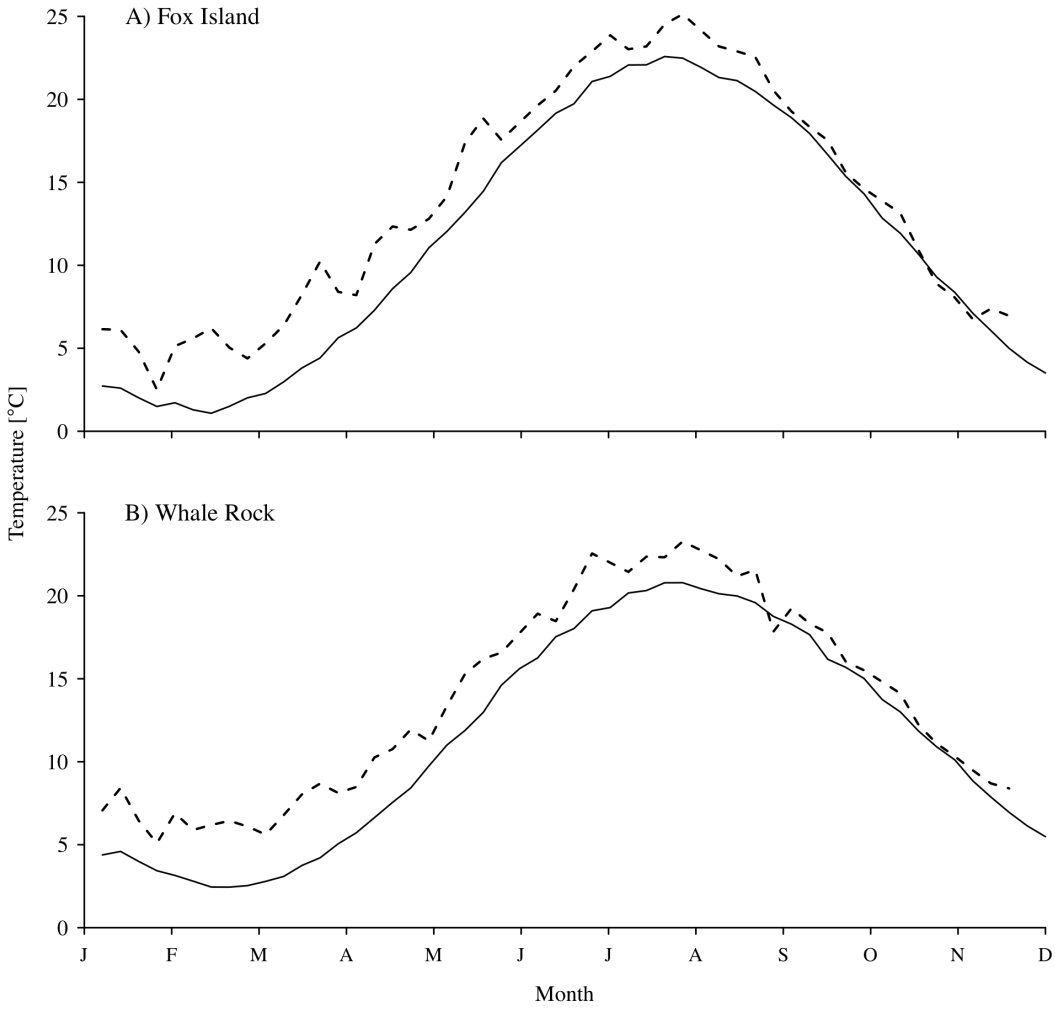


Figure 17. Mean weekly sea surface temperatures from 2007-2011 (solid) and 2012 (dashed) at Fox Island (a) and Whale Rock (b).

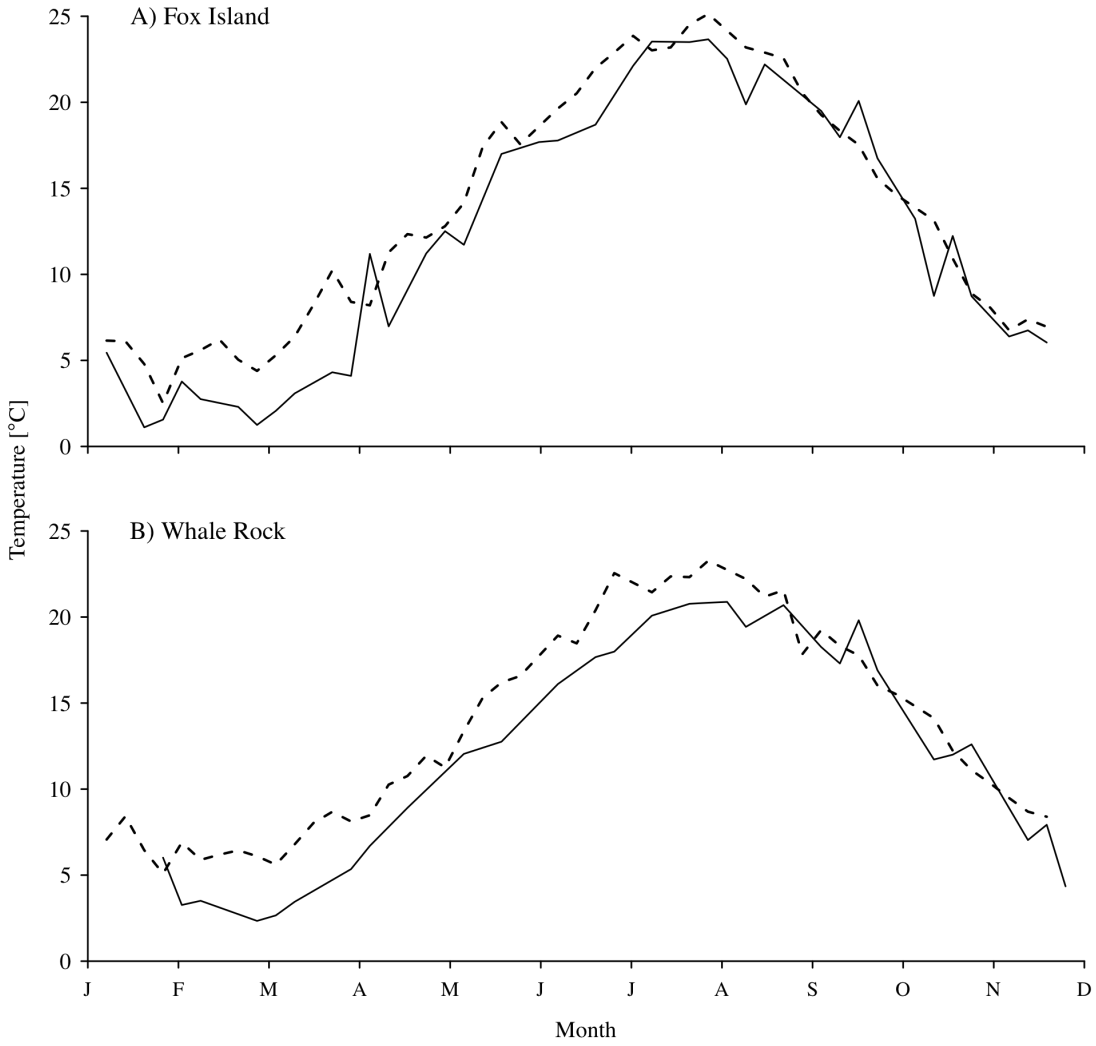


Figure 18. A comparison of 2007-2011 (solid) and 2012 (dashed) mean weekly catch per tow of the dominant species from Fox Island (a) and Whale Rock (b) and the cumulative distributions at each station (c, d).

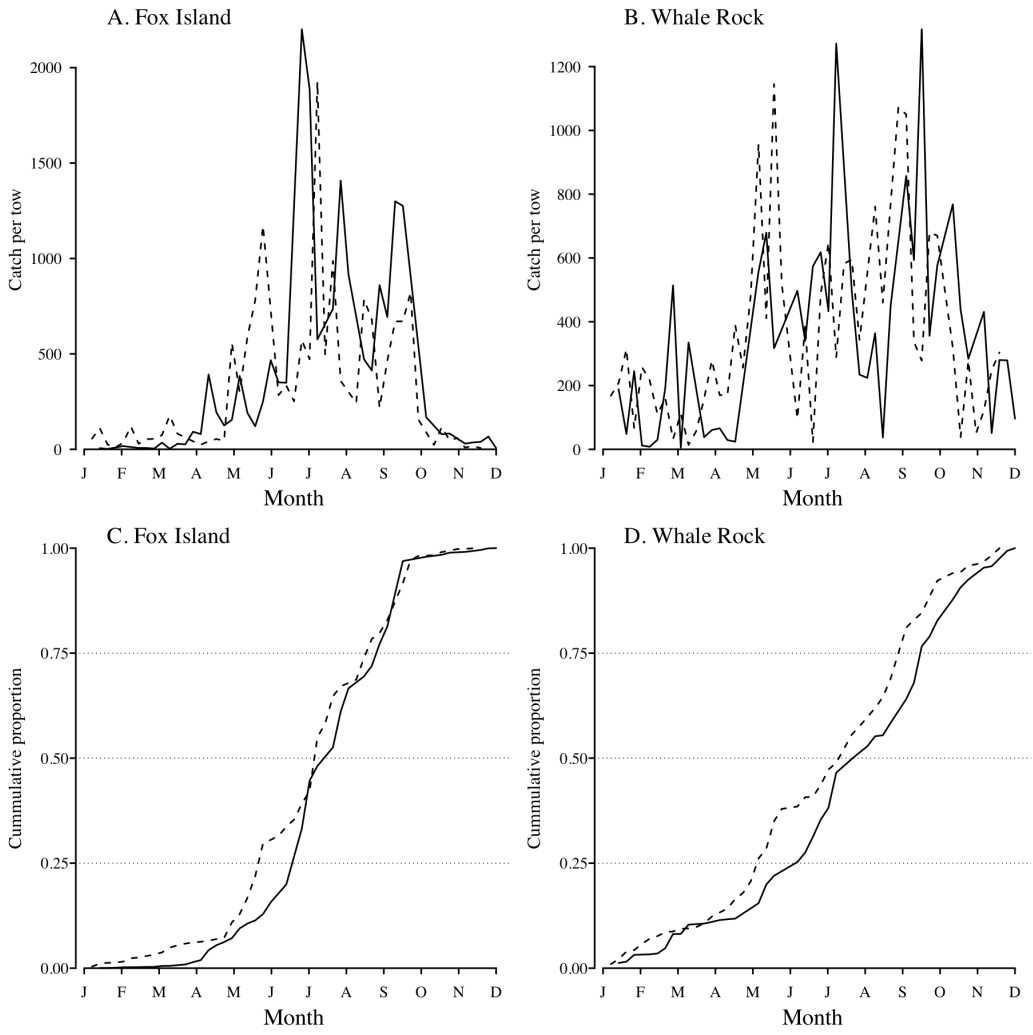


Figure 19. A comparison of 2007-2011 (solid) and 2012 (dashed) mean weekly catch per tow of the warm-water species from Fox Island (a) and Whale Rock (b) and the cumulative distributions at each station (c, d).

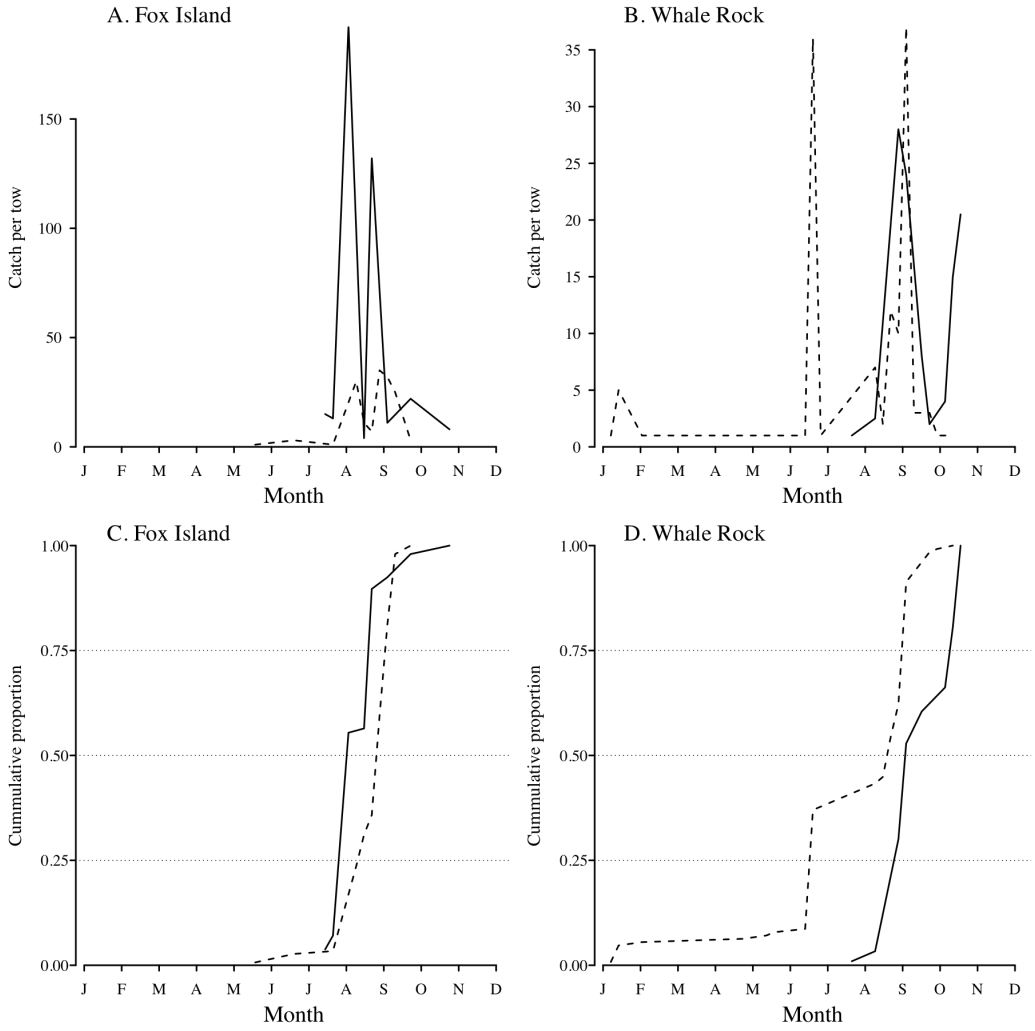


Figure 20. Weekly mean sea surface temperature (red) and chlorophyll (black) concentration at Fox Island (1987-2011).

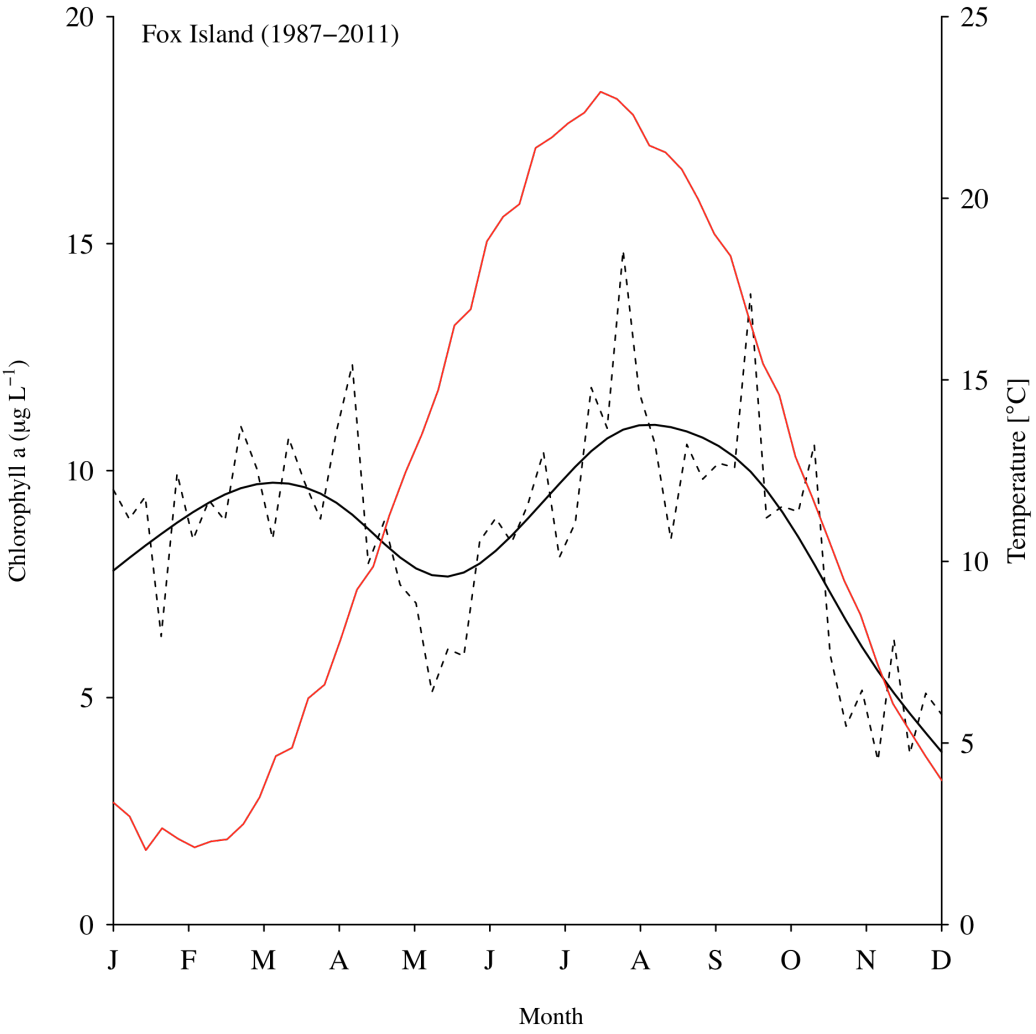
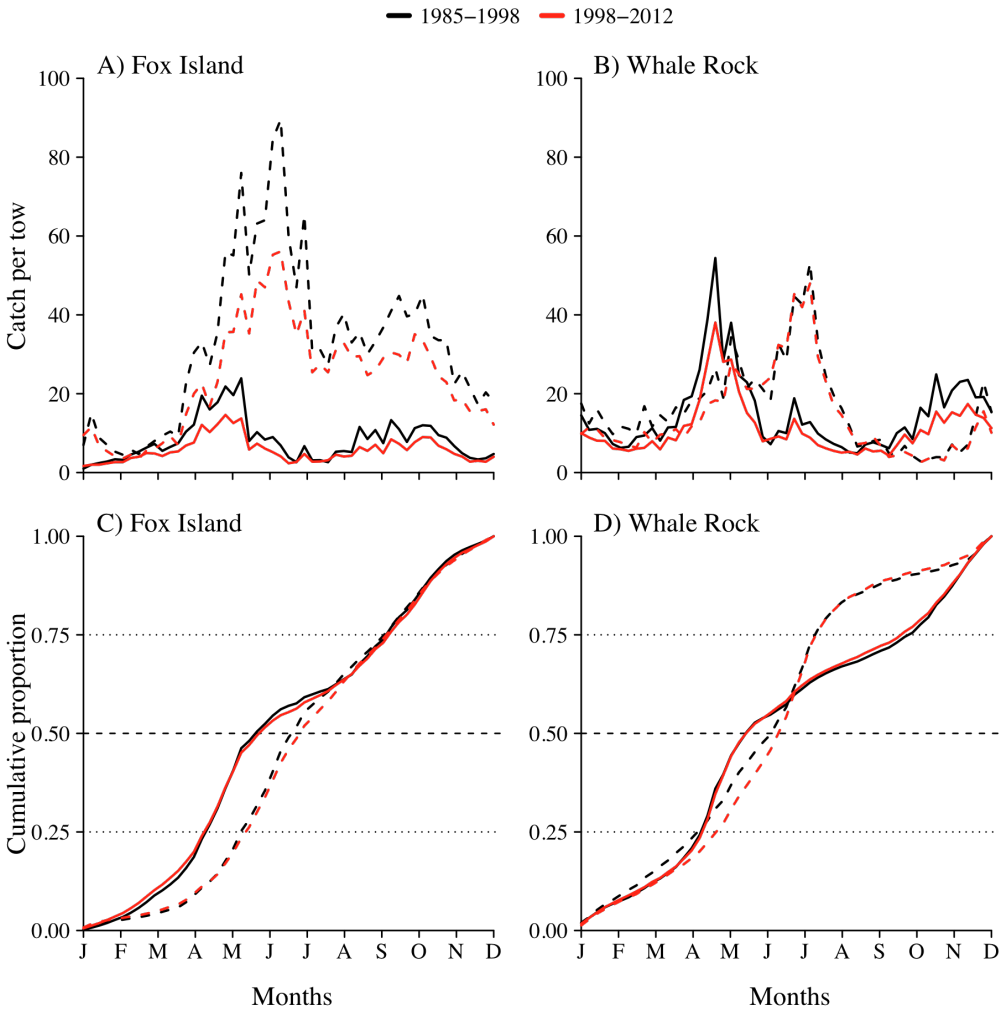


Figure 21. Winter flounder catch per tow abundances at Fox Island (a) and Whale Rock (b) and weekly cumulative proportion of yearly abundances at Fox Island (c) and Whale Rock (d). Winter flounder were sub-divided by size (less than or equal to 20cm, dashed; greater than 20cm, solid).



APPENDIX A

Supplemental Methods

This appendix contains three sections of supplemental methods. The first section supports the Kolmogorov-Smirnov tests used to assess the chlorophyll time series. The second section supports the modified Kolmogorov-Smirnov tests used to determine changing species distributions according to temperature and week of year across the time series split in half. The third section contains figures of temporal trends in species abundances since 1961 at Fox Island and Whale Rock.

SECTION 1: CHLOROPHYLL

Time series of chlorophyll concentrations from the mid and lower bay, Fox Island and the GSO dock respectively, were assessed for spatial and temporal differences in the bay.

Over one thousand repetitions, years were divided randomly to generate two cumulative distributions of chlorophyll concentrations by either weeks or temperatures. Absolute values of the maximum distances between distributions were calculated and used to generate one-tailed frequency distributions. The 95^{th} percentile of each distribution provided a test statistic to compare with the maximum distances generated by dividing the time series in half (1961-1986 and 1986-2012). The following series of figures show the observed distributions (Fig. A-1; Fig. A-2) and the randomly generated maximum distance frequency distributions, quantiles (shaded

areas), and observed maximum distance values (solid vertical lines) (Fig. A-3; Fig. A-4).

Figure A-1. Cumulative distributions of chlorophyll concentration by temperature degree bins used in Kolmogorov-Smirnov testing. (a) A standard Kolmogorov-Smirnov comparison of the full time series for the upper bay station and GSO dock indicated significant differences in the seasonal distribution of chlorophyll (p=0.018, K=0.0.076). Kolmogorov-Smirnov tests based on randomly generated maximum distance distributions were used to compare the first and second halves of Fox Island (b) and GSO dock (c) time series (see Figure 15).

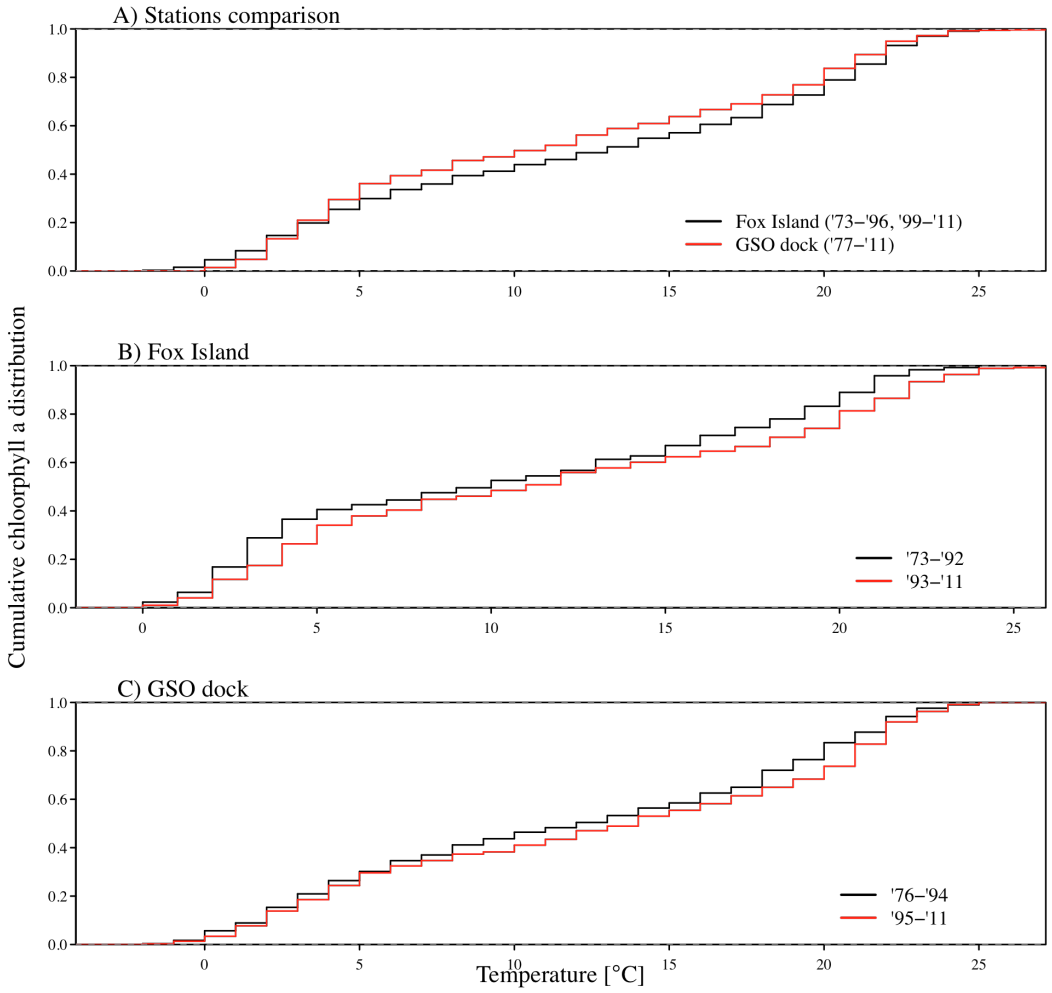


Figure A-2. Cumulative distributions of chlorophyll concentration by weeks used in Kolmogorov-Smirnov testing. (a) A comparison of the full time series for the upper bay station and GSO dock indicated significant differences in the seasonal distribution of chlorophyll (p=0.048, K=0.096). Kolmogorov-Smirnov tests based on randomly generated maximum distance distributions were used to compare the first and second halves of Fox Island (b) and GSO dock (c) time series (see Figure 11).

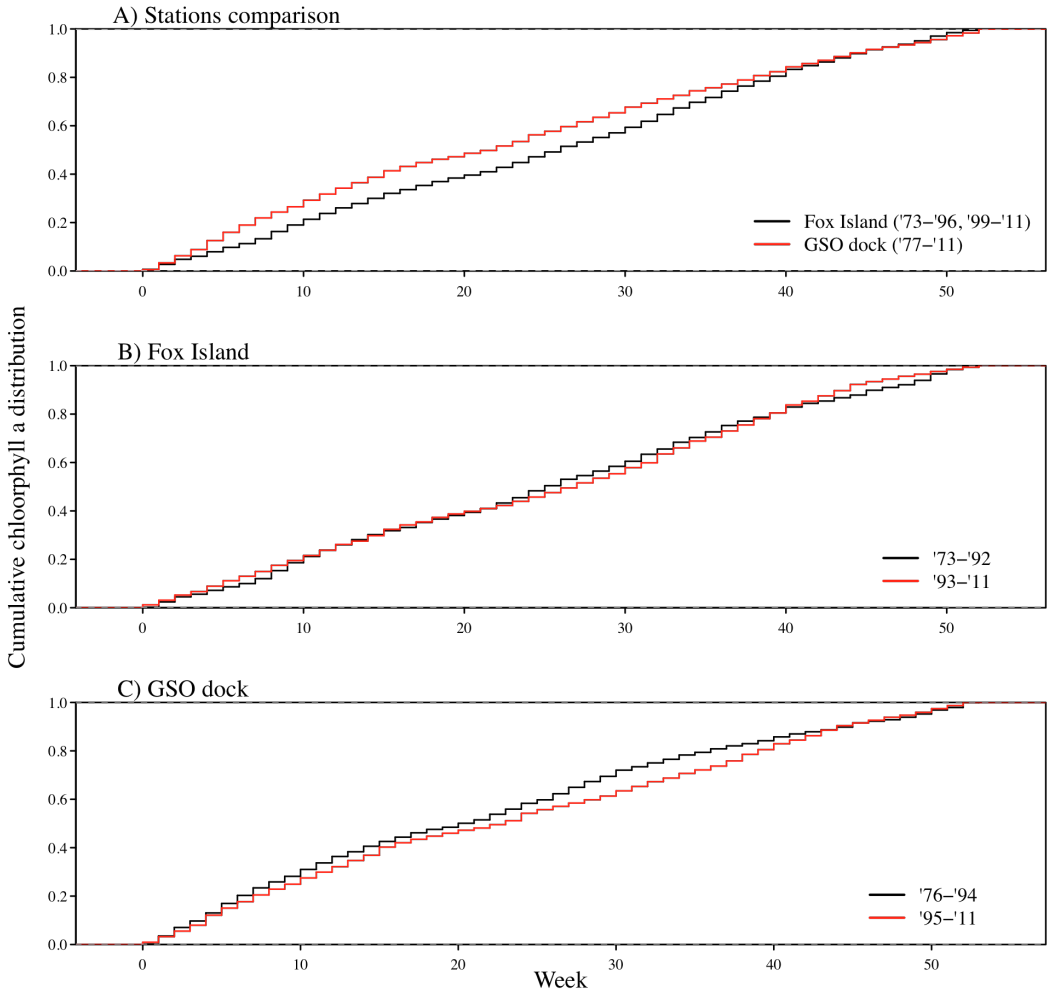


Figure A-3. Maximum distance distributions for randomly split time series at Fox Island (a) and the GSO dock (b). The solid vertical lines indicate observed maximum distance values. According to the randomized years testing, neither station's distribution significantly changed. Fox Island (a) was nearly significantly different (p=0.059, K=0.097).

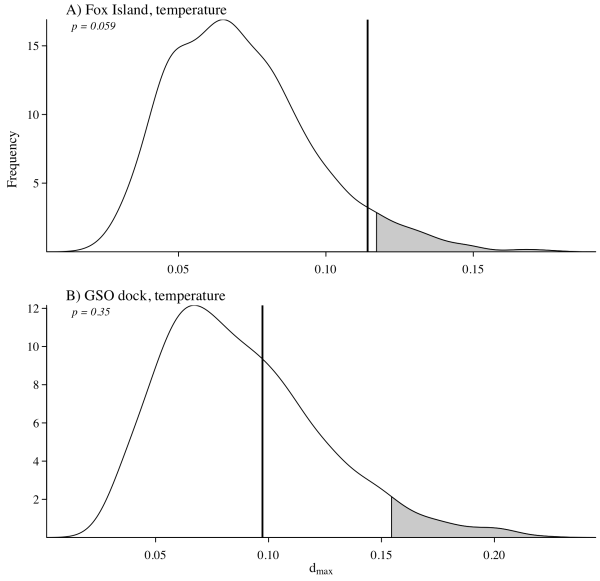
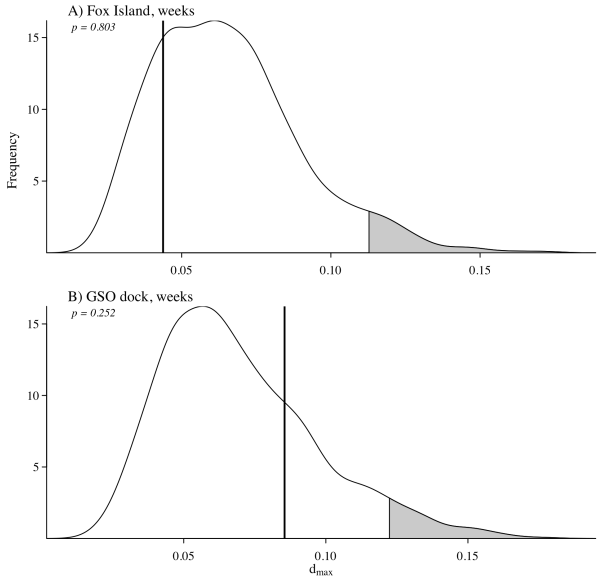


Figure A-4. Maximum distance distributions for randomly split time series at Fox Island (a) and the GSO dock (b). The solid vertical lines indicate observed maximum distance values. According to the randomized years testing, neither station's distribution significantly changed.

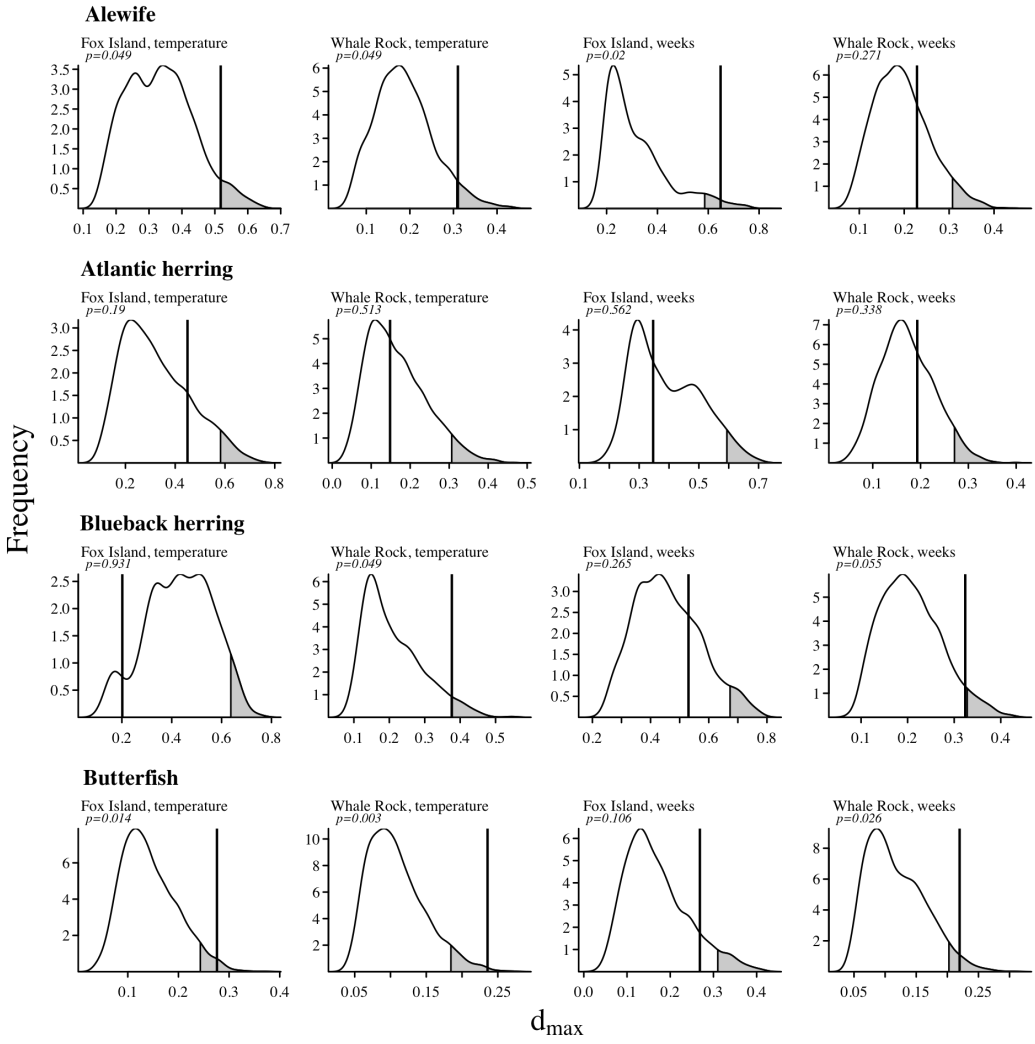


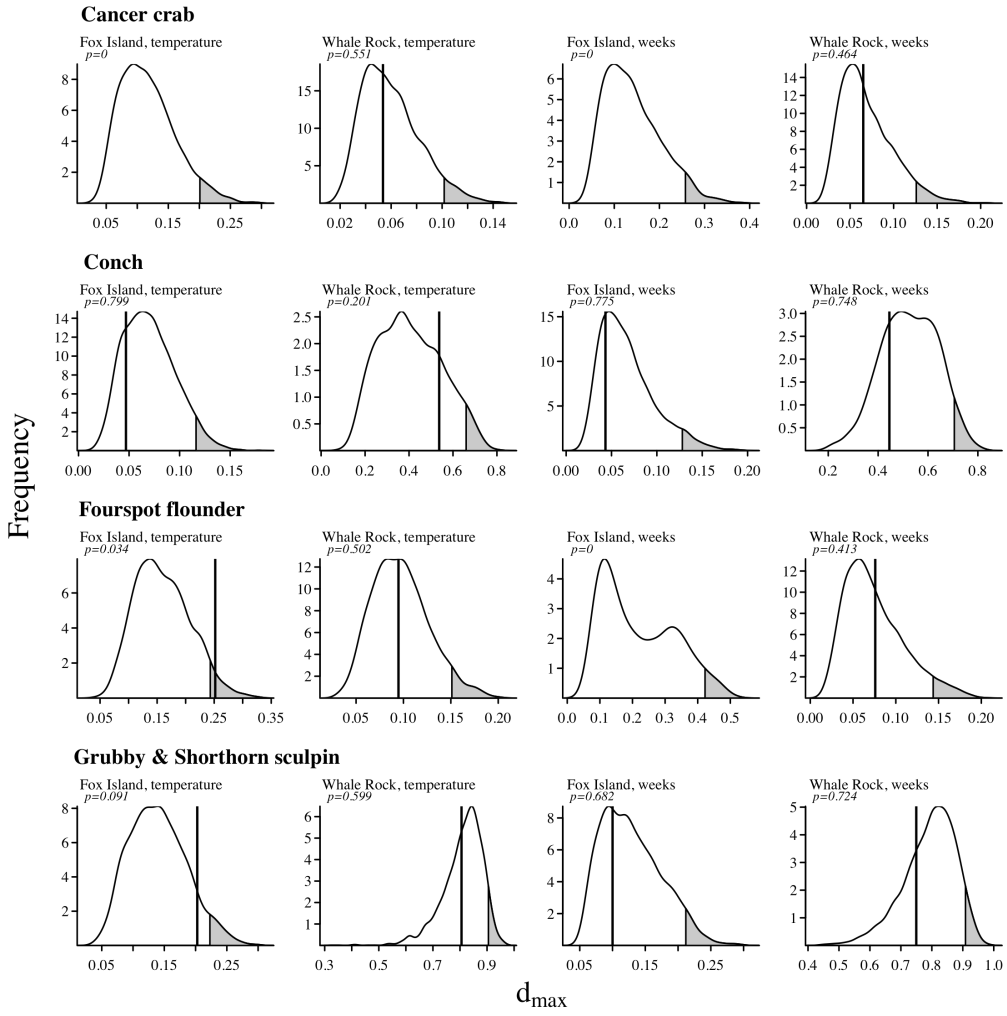
SECTION 2: SPECIES PREFERENCE

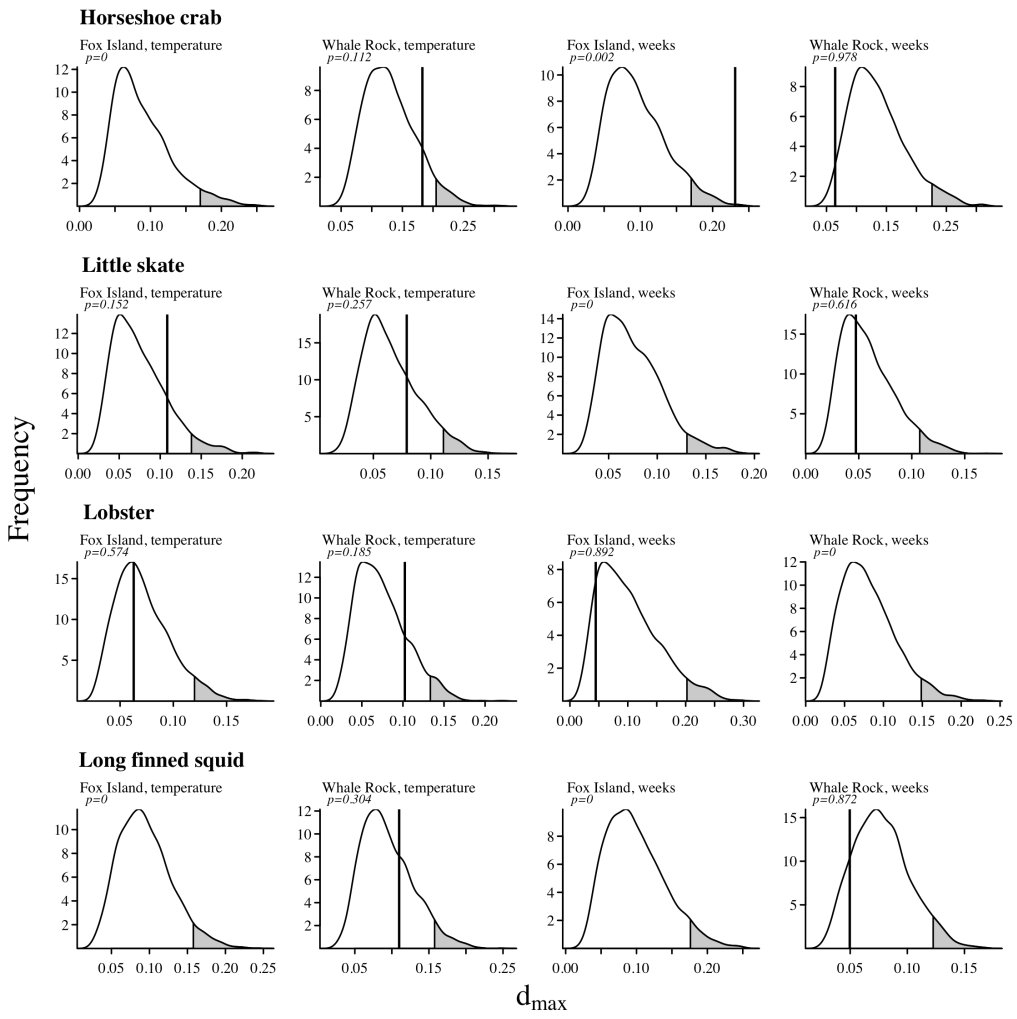
Over one thousand repetitions, years were divided randomly to generate two cumulative distributions of species abundances at each station by weeks and temperatures. Absolute values of the maximum distances between distributions were calculated and used to generate one-tailed frequency distributions. The 95th quantile of each distribution comprised a test statistic used to compare maximum distances generated by the normally divide time series (1961-1986 and 1986-2012). The following series figures shows the frequency distributions, quantiles (shaded areas),

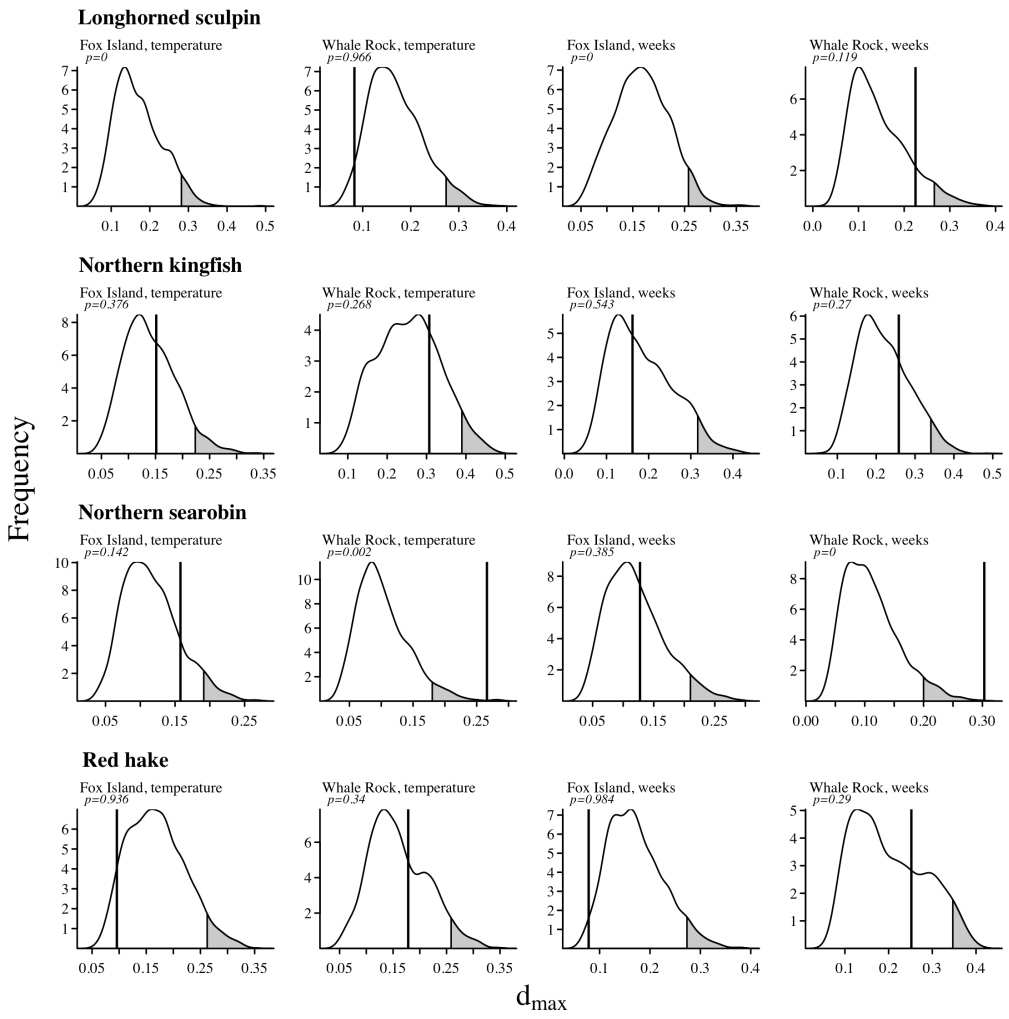
and observed maximum distance values (solid vertical lines). Each row of four figures describes one species' tests. Test values correspond to table 2.

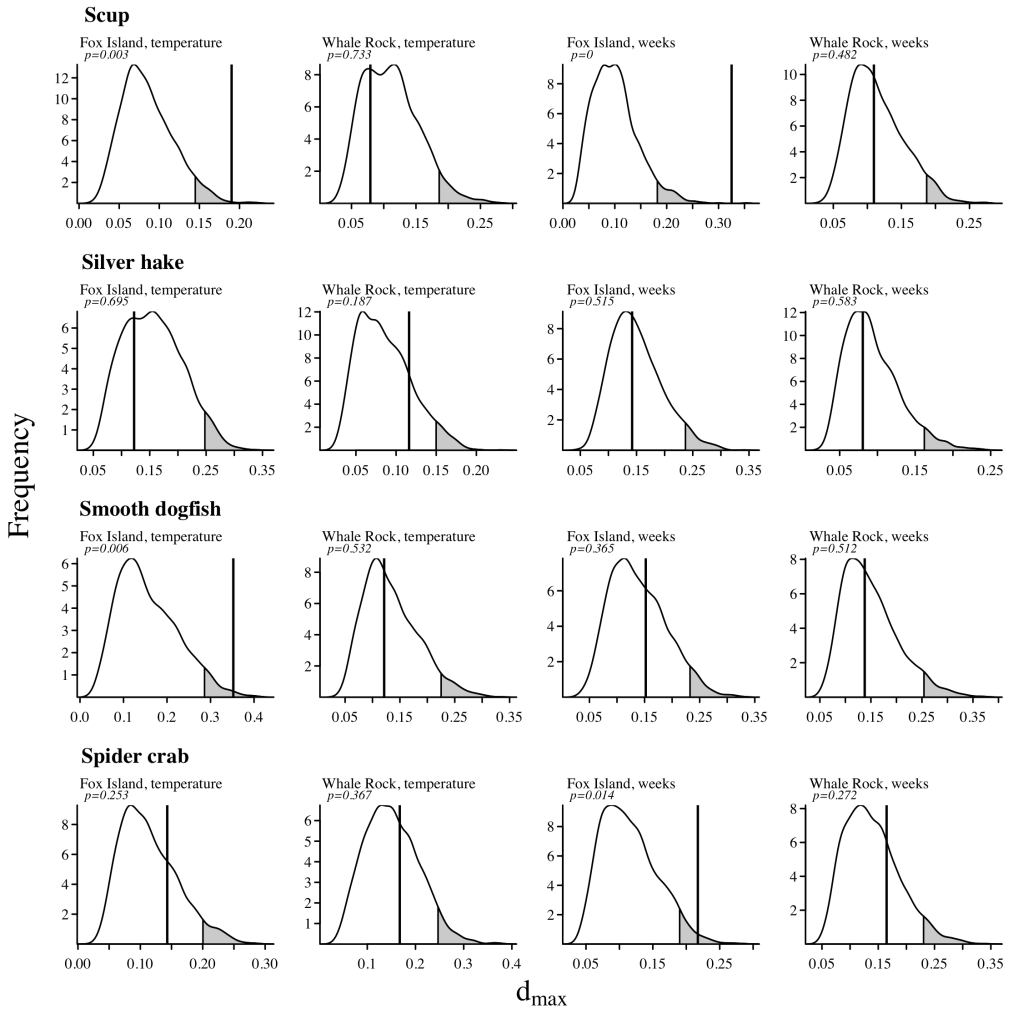
Figure A-5. Modified Kolmogorov-Smirnov test of maximum distance frequency distributions with 95th percentile rejection regions (shaded areas) and observed maximum distance values (solid vertical lines) of dominant species abundances by week of year and temperature from Fox Island and Whale Rock.

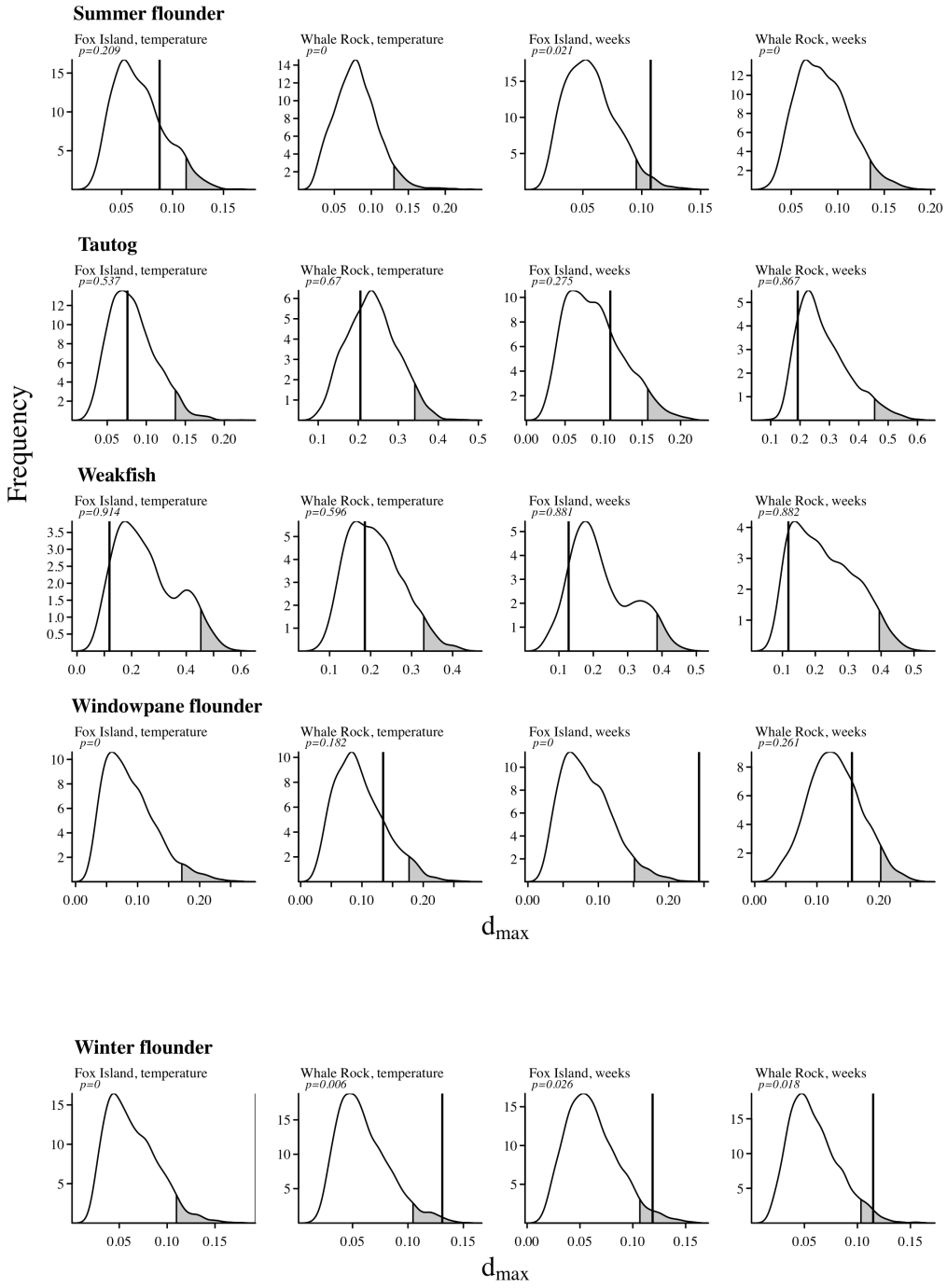



Cancer crab
Fox Island, temperature
p=0
Whale Rock, temperature
p=0.551
Fox Island, weeks
p=0
Whale Rock, weeks
p=0.464
Conch
Fox Island, temperature
p=0.799
Whale Rock, temperature
p=0.201
Fox Island, weeks
p=0.775
Whale Rock, weeks
p=0.748
Fourspot flounder
Fox Island, temperature
p=0.034
Whale Rock, temperature
p=0.502
Fox Island, weeks
p=0
Whale Rock, weeks
p=0.413
Grubby & Shorthorn sculpin
Fox Island, temperature
p=0.091
Whale Rock, temperature
p=0.599
Fox Island, weeks
p=0.682
Whale Rock, weeks
p=0.724
Frequency
dmax


Horseshoe crab
Fox Island, temperature
p=0
Whale Rock, temperature
p=0.112
Fox Island, weeks
p=0.002
Whale Rock, weeks
p=0.978
Little skate
Fox Island, temperature
p=0.152
Whale Rock, temperature
p=0.257
Fox Island, weeks
p=0
Whale Rock, weeks
p=0.616
Lobster
Fox Island, temperature
p=0.574
Whale Rock, temperature
p=0.185
Fox Island, weeks
p=0.892
Whale Rock, weeks
p=0
Long finned squid
Fox Island, temperature
p=0
Whale Rock, temperature
p=0.304
Fox Island, weeks
p=0
Whale Rock, weeks
p=0.872
Frequency
dmax


Longhorned sculpin
Fox Island, temperature
p=0
Whale Rock, temperature
p=0.966
Fox Island, weeks
p=0
Whale Rock, weeks
p=0.119
Northern kingfish
Fox Island, temperature
p=0.376
Whale Rock, temperature
p=0.268
Fox Island, weeks
p=0.543
Whale Rock, weeks
p=0.27
Northern searobin
Fox Island, temperature
p=0.142
Whale Rock, temperature
p=0.002
Fox Island, weeks
p=0.385
Whale Rock, weeks
p=0
Red hake
Fox Island, temperature
p=0.936
Whale Rock, temperature
p=0.34
Fox Island, weeks
p=0.984
Whale Rock, weeks
p=0.29
Frequency
dmax


Scup
Fox Island, temperature
p=0.003
Whale Rock, temperature
p=0.733
Fox Island, weeks
p=0
Whale Rock, weeks
p=0.482
Silver hake
Fox Island, temperature
p=0.695
Whale Rock, temperature
p=0.187
Fox Island, weeks
p=0.515
Whale Rock, weeks
p=0.583
Smooth dogfish
Fox Island, temperature
p=0.006
Whale Rock, temperature
p=0.532
Fox Island, weeks
p=0.365
Whale Rock, weeks
p=0.512
Spider crab
Fox Island, temperature
p=0.253
Whale Rock, temperature
p=0.367
Fox Island, weeks
p=0.014
Whale Rock, weeks
p=0.272
Frequency
dmax


Summer flounder
Fox Island, temperature
p=0.209
Whale Rock, temperature
p=0
Fox Island, weeks
p=0.021
Whale Rock, weeks
p=0
Tautog
Fox Island, temperature
p=0.537
Whale Rock, temperature
p=0.67
Fox Island, weeks
p=0.275
Whale Rock, weeks
p=0.867
Weakfish
Fox Island, temperature
p=0.914
Whale Rock, temperature
p=0.596
Fox Island, weeks
p=0.881
Whale Rock, weeks
p=0.882
Windowpane flounder
Fox Island, temperature
p=0
Whale Rock, temperature
p=0.182
Fox Island, weeks
p=0
Whale Rock, weeks
p=0.261
Frequency
dmax
Winter flounder
Fox Island, temperature
p=0
Whale Rock, temperature
p=0.006
Fox Island, weeks
p=0.026
Whale Rock, weeks
p=0.018
dmax

SECTION 2: TEMPORAL TRENDS IN SPECIES ABUNDANCES

This section contains linear regressions of the log transformed annual mean abundance (1961-2012) of each species.

Figure A-6. Linear regressions of log-transformed annual mean abundances by species at Fox Island.

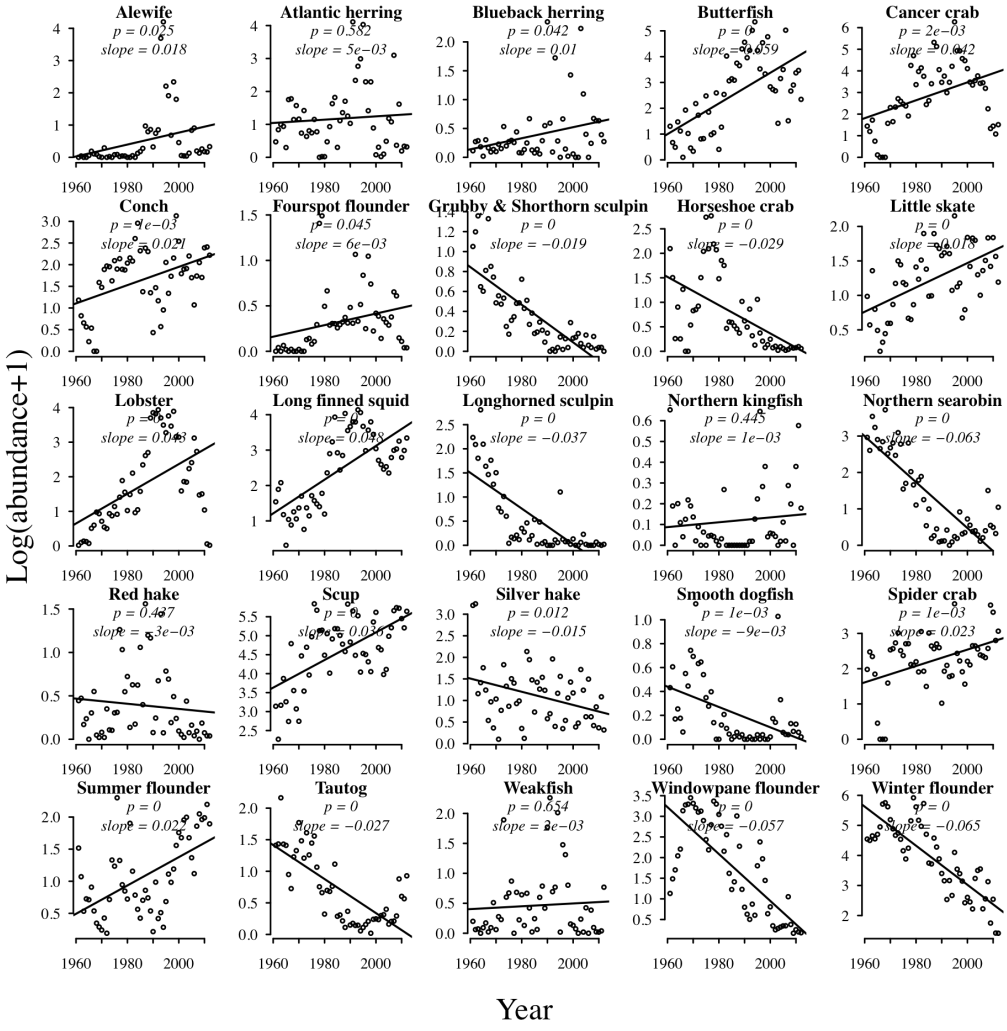
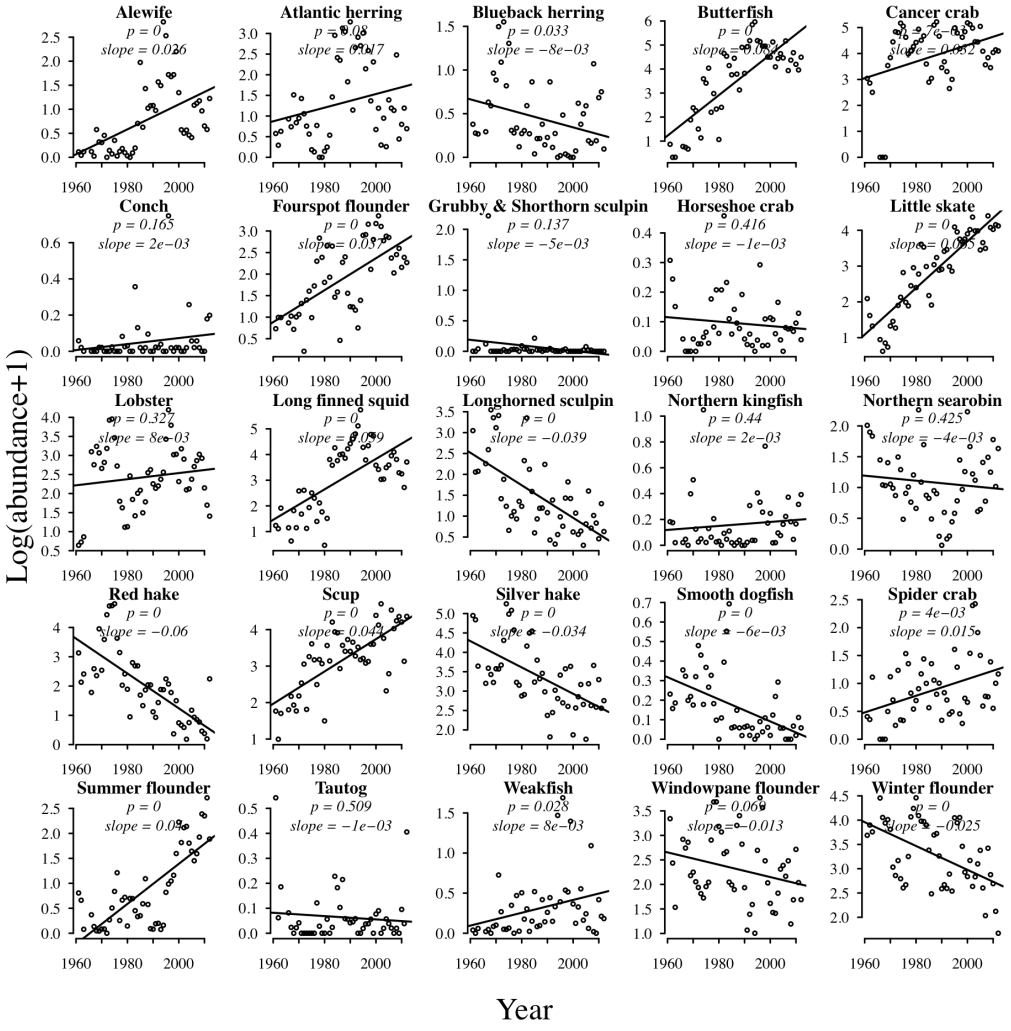


Figure A-7. Linear regressions of log-transformed annual mean abundances by species at Whale Rock.



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